

## MYCOTAXON

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**Studies in *Amanita* (Amanitaceae) of Central America. 1.  
Three new species from Costa Rica and Honduras**R.E. TULLOSS<sup>1,a</sup>, R.E. HALLING<sup>b</sup> & G.M. MUELLER<sup>c</sup><sup>a</sup>*P. O. Box 57, Roosevelt, New Jersey 08555-0057, USA*<sup>b</sup>*The New York Botanical Garden, Bronx, New York 10458, USA*<sup>c</sup>*Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, USA*CORRESPONDENCE TO: [ret@eticomm.net](mailto:ret@eticomm.net), [rhalling@nybg.org](mailto:rhalling@nybg.org), & [gmueller@chicagobotanic.org](mailto:gmueller@chicagobotanic.org)

**ABSTRACT**—*Amanita conara*, *A. costaricensis*, and *A. garabitoana* are proposed as new species. These taxa are added to twelve previously described species known from, or reported here for the first time from, the region of study: *A. advena*, *A. arocheae*, *A. brunneolocularis*, *A. colombiana*, *A. eburnea*, *A. farinosa*, *A. flavoconia* var. *inquinata*, *A. fulgineodisca*, *A. muscaria* subsp. *flavivolvata*, *A. polypyraxis*, *A. sororcula*, and *A. xyliniivolvata*. *Amanita flavoconia* var. *sinapicolor* is proposed to be a taxonomic synonym of *A. flavoconia* var. *inquinata*. An unusual species of *Amanita* subsection *Vittadiniae* is given the code *Amanita* sp. HON1 and treated only in a key to regional species of *Amanita* section *Lepidella*. A gazetteer is provided for Costa Rican sites at which *Amanita* species have been collected.

**KEY WORDS**—Área de Conservación Guanacaste, Cordillera Talamanca, Mexico, Andean Colombia, taxonomy

**Introduction and overview**

This paper addresses the genus *Amanita* Pers. as a part of the extensive study of macromycetes undertaken by Halling, Mueller, and numerous colleagues in Costa Rica.

The history of work investigating the diversity of Costa Rican macrofungi [see discussions in (Halling & Franco-M. 1996; Halling & Mueller 1999, 2005; Baroni and Halling 2000; Ammirati et al. 2007)] has been long, but intermittent. Currently there is an emphasis on obtaining additional data on the fungi of Costa Rica through the Costa Rican National Biodiversity Inven-

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Fig. 1. *Amanita garabitoana*. a. Habit (Halling 8198) ( $\times 0.25\pm$ ). b. Habit (holotype) ( $\times 0.27$ ). Photos by R.E. Halling (a) and R.E. Tulloss (b).

tory—a multinational project coordinated by the Costa Rican National Biodiversity Institute (INBio) (Mueller & Mata 2001). Work to date has documented a highly diverse macrofungal community (Mueller & Halling 1995; Carranza & Mueller 1996; Halling & Mueller 1997, 2002; Mueller et al. 2006). To date our investigation of Costa Rican *Amanitaceae* indicates there are at least 35 species of *Amanita* in the country; of these, a number will be new to science.

## Materials and Methods

Methods and terminology follow those of Tulloss et al. (1992) and expansions by Tulloss (1993, 1994, 1998b, 2000a). A recent terminological summary appeared in (Tulloss & Lindgren 2005) and is available on-line (Tulloss 2011a).

Samples from selected exsiccata revised during research reported herein have been supplied to three laboratories now carrying out phylogenetic studies related to *Amanita* sections *Caesareae* and *Lepidella*.

Color codes of the form “6D6” are from (Kornerup & Wanscher 1978). Color codes of the form “10YR 4/3” are from the Munsell soil color charts (Anonymous 1975). Color codes of the form created by the Inter-Society Color Council and the U.S. National Bureau of Standards were translated to Munsell notation using (Kelly 1965; McKnight 1977). Color names with initial capital letters (e.g., Empire Yellow) are from Ridgway (1912), and conversions from Ridgway’s names to Munsell color codes is based on the work of Hamly (1949).

The form of author citations follows Kirk & Ansell (1992, 2010).

“P. N.” stands for “Parque Nacional.” The nonitalicized abbreviation “std.” stands for “standard deviation.” With two exceptions (“HKAS”—Kunming Institute of Botany, Academia Sinica, China; and “RET”—Tulloss’ personal herbarium), codes for herbaria follow Index Herbariorum (Holmgren et al. 1990; Thiers 2010).

In the lists of collections examined, locality names in Costa Rica are provided in abbreviated form. Known site data for these abbreviated names are provided in the appendix to this paper.

## Taxonomic part

Extensive collecting in Costa Rica in the last fifteen years has much improved understanding of the genus *Amanita* in that country. We estimate the number of species in the genus present in Costa Rica alone to be 35 to 40. To date, 12 previously described taxa of *Amanita* have been collected and determined or described as new from Costa Rica and Honduras. Previously described taxa are provided in the following list—organized by section of the genus. When range data in a list entry includes Colombia, the source is Tulloss et al. (1992).

*Amanita* sect. *Amanita* (three taxa):

- *A. farinosa* Schwein. – Costa Rica is the known southern limit of distribution. It was described from North Carolina, USA; the range of this mushroom extends northward into Prov. Québec, Canada (Pomerleau 1980).
- *A. muscaria* subsp. *flavivolvata* Singer – originally described from *ca.* San Francisco, California, USA, this species now is known to have a range extending north into the Alaskan panhandle and eastward across Canada and the northern United States to Newfoundland in the north and extending southward at least to Costa Rica. In the southeastern U.S. its distribution is unclear due to confusion with *A. muscaria* var. *persicina* Dav. T. Jenkins (Jenkins 1977, 1986), which is endemic in that region. In North America, a yellow-capped color-variant of subsp. *flavivolvata* dominates in most of that part of the region of distribution north and east of the Great Plains. The typical, red-capped color-variant dominates throughout the remainder of the range. In the neovolcanic region of Mexico, the subspecies is relatively common in mixed montane forest; and is associated with *Quercus* in Costa Rica. If not native in Colombia, it has been introduced there with *Pinus* or *Quercus* from more northerly latitudes. The taxon is often misreported throughout its range as the type subspecies or type variety of *A. muscaria* (L. : Fr.) Lam. (Tulloss 2009c; Geml et al. 2008).

- *A. xylinvolve* Tulloss, Ovrebo & Halling – This species was described from Andean Colombia. Cochise Co., Arizona, is the known northern distribution limit (Tulloss 2011b).

*Amanita* sect. *Caesareae* Singer: no previously described taxa known.

*Amanita* sect. *Vaginatae* sensu Zhu L. Yang (Yang 1997) (three taxa):

- *A. colombiana* Tulloss, Ovrebo & Halling – Costa Rica is the known northern limit of distribution. The southern limit is in Andean Colombia.
- *A. fuligineodisca* Tulloss, Ovrebo & Halling – Honduras is the known northern limit of distribution. The southern limit is in Andean Colombia.
- *A. sororcula* Tulloss, Ovrebo & Halling – Costa Rica is the known northern limit of distribution. The southern limit is in Andean Colombia.

*Amanita* sect. *Lepidella* sensu Bas (1969) (two taxa):

- *A. advena* Tulloss, Ovrebo & Halling – Costa Rica is the known northern limit of distribution. The southern limit is in Andean Colombia. Previous to our work in Costa Rica, the only known collection of this species was the Colombian holotype.
- *A. polypyramis* (Berk. & M. A. Curtis) Sacc. – Costa Rica is the southern limit of known distribution. The known northern limit is in the sandy Atlantic coastal plane of Cape Cod, Massachusetts (Tulloss 2009b). The species was described from North Carolina.

*Amanita* sect. *Amidella* (E.-J. Gilbert) Konrad & Maubl.: no previously described taxa known.

*Amanita* sect. *Phalloideae* (Fr.) Quél. (two taxa):

- *A. arocheae* Tulloss, Ovrebo & Halling – No change in known range (central Mexico to Andean Colombia).
- *A. eburnea* Tulloss (Tulloss 1989) – No change in known range (Belize and Honduras).

*Amanita* sect. *Validae* (Fr.) Quél. (two taxa):

- *A. brunneolocularis* Tulloss, Ovrebo & Halling – This species was originally described from Costa Rica and Colombia. It has now been found under *Pinus* in North Carolina, USA, along a well-traveled highway (Tulloss 2009d).
- *A. flavoconia* var. *inquinata* Tulloss, Ovrebo & Halling – The known northern limit of the range of this taxon is in the neovolcanic zone of central Mexico. Field observation in Costa Rica has led us to conclude that *A. flavoconia* var. *sinapicolor* Tulloss, Ovrebo & Halling comprises material of var. *inquinata* that has been exposed to direct sun-

light at higher altitudes resulting in some desiccation and alteration of pigment. As has been observed in other taxa of *Amanita* (e.g., Tulloss & Borgen 1996; Tanghe & Hillhouse 1973), the desiccation also results in production of smaller and more nearly globose spores. As previously observed, (Tulloss et al. 1992), there is a strong statistical correlation between cap color and spore shape; but we now believe this was wrongly interpreted as genetically determined by the authors of the pale variety. Therefore, we propose reducing *A. flavoconia* var. *sinapi-color* to synonymy with var. *inquinata*.

### 1. Section *Caesareae*

At present we believe that there are as many as 3 taxa of *Amanita* sect. *Caesareae* in Costa Rica (Tulloss 2009e). These include no taxa known previously from Andean Colombia (Tulloss et al. 1992). In this paper we propose a new species easily distinguishable in the field, in *Amanita* stirps *Hemibapha* (Tulloss 1998a, Tulloss 2009a)—*A. garabitoana*.

*Amanita garabitoana* Tulloss, Halling & G.M. Muell. sp. nov.

FIGS. 1–4

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Fig. 2. *Amanita garabitoana*. Habit (Tulloss 6-16-95-D), (a.  $\times 0.38$ . b.  $\times 0.31$ ). Photos by R.E. Tulloss.

*Pileus* 60–212 mm *latus*, *aurantiobrunneus vel olivaceoflavus vel flavobrunnea vel aurantioflava*, *disco olivaceobrunneo vel aurantiobrunneo vel rubrobrunneo*, *saepe zona brunnea circa ad extremum striae marginalium*, *marginē longistriato*, *nonappendiculato*. *Lamellae subadnatae vel liberae, confertae, subroseocremae vel subaurantiocremae vel pallidocremae vel subalbae vel albae; lamellulae subtruncatae vel truncatae*. *Stipes* 95–258 × 15–24 mm, *subaurantioflavus vel pallidobubalinus vel subcremeus*, *bulbo nullo, annulatus, frustris coactis flavis vel sordido flavis vel olivaceoflavis vel brunneis vel aurantiis partis superae limbi interni veli universalis ornatus; velum universali saccatum, robustum, membranosum*, 48–96 × 30–45 mm, *pagina externa alba, pagina interiori subaurantia vel pallidobrunnea*. *Fibulae praevalgaris*. *Basidiosporae* (7.5–) 8.0–11.0 (–13.6) × (5.7–) 6.5–8.4 (–9.9)  $\mu\text{m}$ , (*L* = (8.3–) 8.7–10.0 (–10.3)  $\mu\text{m}$ ; *L'* = 9.4  $\mu\text{m}$ ; *W* = (6.6–) 6.9–7.7 (–7.8)  $\mu\text{m}$ ; *W'* = 7.3  $\mu\text{m}$ ; *Q* = (1.06–) 1.15–1.43 (–1.73); *Q* = (1.22–) 1.24–1.37 (–1.40); *Q'* = 1.29), *nonamyloideae, late ellipsoideae vel ellipsoideae*. *In quercetis tropicalibus montanis costaricensibus et hondurensibus habitat*. *Amanita arkansana Amanitae stirpis Hemibaphae simulanissima*. *Species nova ob distributionem geographicam, pileum et stipem relative robustiores, ordinationem colores, colores variabiles ob aetatem vel contusa, et magnitudinem sporarum*.

**HOLOTYPE** — Costa Rica, Prov. San José, San Gerardo de Dota no. 1, Tulloss 6-21-95-G (USJ).

**ETYMOLOGY** — In honor of Garabito, an indigenous military-political leader of the Huetares, a people of the Central Valley of Costa Rica. Garabito resisted Spanish occupation of Costa Rica until his capture in 1574. He fought to maintain the cultural heritage of his people and to oppose both the mistreatment of indigenous peoples by the Spanish and the establishment of Catholicism.

**ILLUSTRATIONS:** Rossman, et al. (1998: cover [Tulloss 6-16-95-D]); Tulloss (2000: 16 (fig. on right) [Tulloss 6-16-95-D]); Halling & Mueller (2005: 32 [Halling 8138], 173 [Halling 8438]).

**PILEUS:** 60–212 mm wide, orange-brown (e.g., 5C6-7) to olivaceous yellow or yellowish brown (4B-C7) to olivaceous tan (more orange than 4B8) to orangish yellow (4A6), darker over disc [e.g., olive brown (more olivaceous than 5D7-8) to orange-brown (6C8) to red-brown (6E6-7, 10F5)], often with dark zone (brown to chestnut brown) at inner end of marginal striations, drying dark brown, campanulate to strongly convex to convex to planoconvex with slightly depressed disc, with large broadly subconic umbo, viscid to tacky to dry (then subshiny), often dull, subglabrous to glabrous, silky fibrillose to fibrillose to somewhat finely pruinose over disc; *context* white to pale sordid white to pale yellowish white outside of disc, yellow (3A3) to pale yellow under pileipellis and above stipe in disc or above lamellae, 4.5–12.5 mm thick at stipe, thinning evenly for 75–85% of radius, then membranous to margin; *margin* strongly striate to plicate-striate [(0.15R–) 0.5R–0.75R], incurved at first, remaining at least somewhat decurved, rounded serrate to eroded, nonappendiculate; *universal veil* absent.

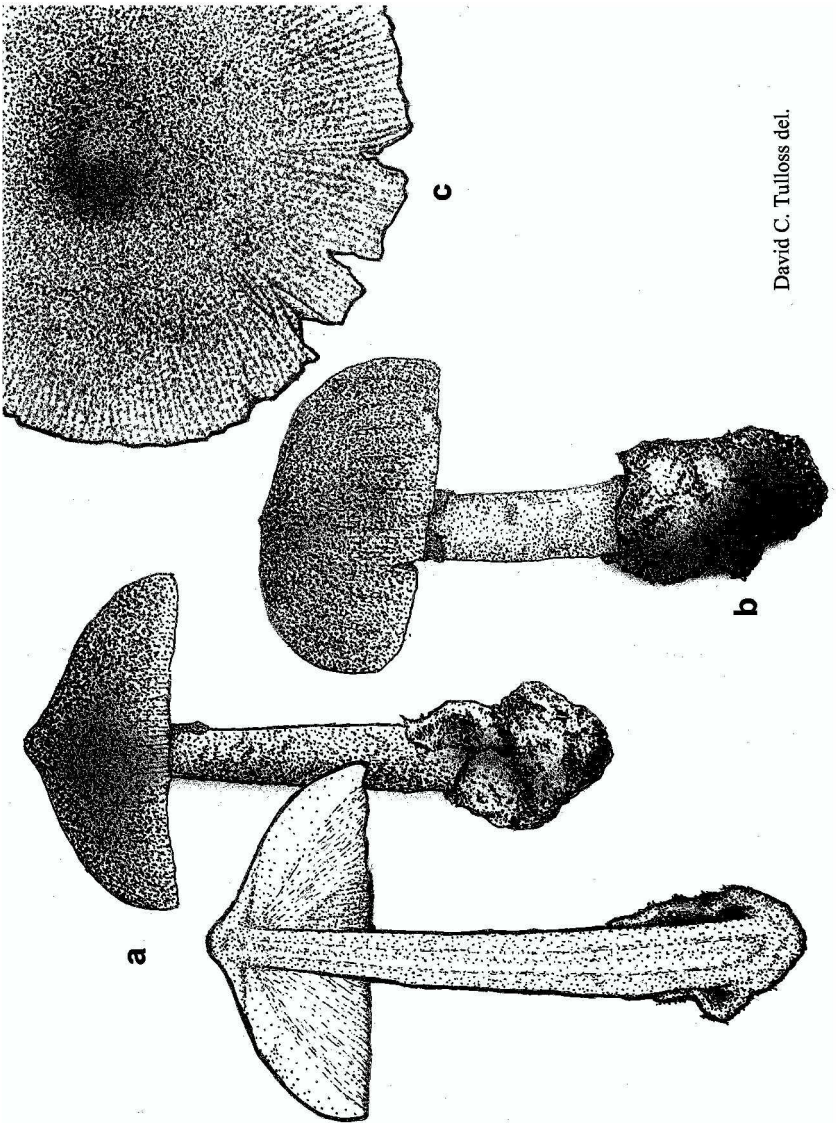


Fig. 3. *Amanita garabitoana* habit. a. Tulloss 6-16-95-D ( $\times 0.33$ ). b. Tulloss 6-15-95-H p.p. ( $\times 0.57$ ). c. Tulloss 6-15-95-H p.p. ( $\times 0.39$ ).

LAMELLAE: adnate to narrowly adnate to free, sometimes with short decurrent line (rarely extending to partial veil, sometimes requiring  $10\times$  lens) on stipe,

close to crowded, faintly pinkish cream to pale orangish cream to pale yellowish cream to light cream to pale yellow to dull white to off-white in mass, white to off-white to pale yellowish white in side view, 4.5–23 mm broad, broadest at about 75% of radius from stipe, thin to moderately thick, with entire and concolorous edge, some forked near margin, with occasional reverse forking; *lamellulae* rounded truncate to subtruncate to truncate (less frequently subattenuate to attenuate, but commonly so in one collection), unevenly distributed, of diverse lengths, plentiful.

**STIPE:** 95–258 × 15–24 mm, with ground color light orangish yellow (ca. 4A5) to pale yellow (3A3) to buff to yellowish white to off-white, yellow and pruinose at apex, unchanging or with ground taking on more orange tint or becoming more sordid with age, cylindric or narrowing upward, barely or not at all flaring at apex, below partial veil decorated with dry ochraceous to dull brownish orange to light orange-brown (5C5) to yellow brown (ca. 4B7-8) to yellow (2A3-4) floccose to fibrillose scales (becoming darker or more orange from handling), below annulus minutely fibrillose or finely striatulate (especially with age); *context* white to pale yellow (2A2) to pale yellow-orange (4A3), unchanging, with larval tunnels concolorous, stuffed with white glistening fibrillose material moderately loosely packed, becoming hollow, with central cylinder 3–10 mm wide; *partial veil* with upper surface light yellow to slightly greenish yellow (3A4) to dull yellow (4A4-5) to sordid yellow (more sordid than 4A8, more sordid than 4B4) to moderate yellow (not as green as 3A4), subsuperior to subapical to apical (e.g., attached for 5± mm, with 3–15 mm free), membranous, thin, copious, skirt-like, persistent, eventually collapsing on stipe and becoming sordid yellow, striate on upper surface, smooth below; *universal veil* as saccate volva almost always connected at (or very near to) base of stipe, often with considerable rather firm portion below stipe base, 48–96 × 30–45 mm (often entirely below substrate surface), membranous, soft, with outer surface white (sometimes with orange-brown discoloration) and inner surface pale olivaceous tan to pale orangish white [may become browner (paler than 10YR 8/6) with age], with context white, 1.5–4± mm thick, with limbus internus not always distinct or well preserved [when present, largely white or largely concolorous with material decorating stipe, at variable distance from point of attachment of volva and stipe, at first firmly connected to sordid yellowish felted material (with latter eventually becoming stipe-decorating squamules and patches)].

*Odor* mild, indistinct, or fungoid. *Taste* indistinct.

**MACROCHEMICAL TESTS:** Laccase test (syringaldazine): in material just maturing, negative throughout basidiome. Tyrosinase test (paracresol): in material

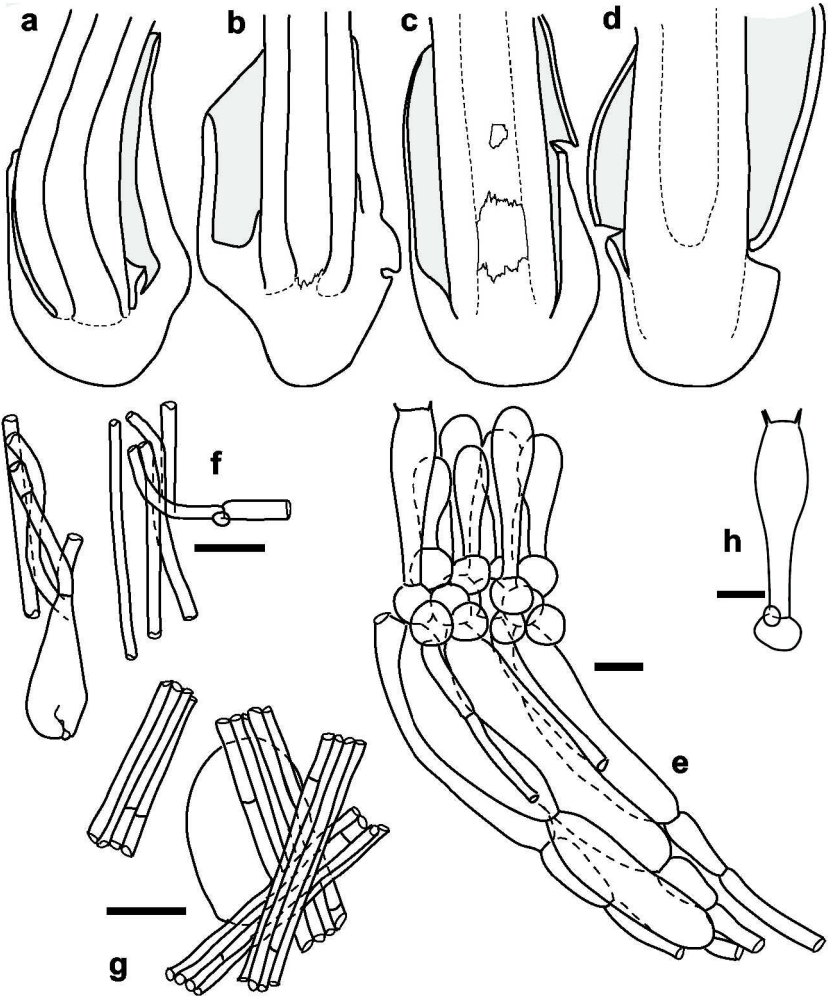


Fig. 4. *Amanita garabitoana*. a-d. Variation of stipe base attachment to universal veil and variation of limbus internus (a. Tulloss 6-16-95-C. b. Tulloss 6-16-95-K. c. holotype. d. Tulloss 6-15-95-H). e. Elements of hymenium and subhymenial tree (isotype). f. Elements of partial veil interior (Schmit 475). g. Elements of partial veil viewed from underside (isotype). h. Basidium with clamp (Tulloss 6-16-95-C). Scale bars = 10  $\mu$ m.

just maturing, positive in cap context, pileipellis, lower half of stipe context, universal veil except for very base of volva, partial veil, and on edges (including breaks and cuts) of lamellae. Test voucher: Tulloss 6-21-95-G.

PILEIPELLIS: 75–100  $\mu\text{m}$  thick; subpellis yellow-orange, 65–90  $\mu\text{m}$  thick; suprapellis minimal, pallidly concolorous to colorless, extensively gelatinized,  $10\pm$   $\mu\text{m}$  thick, intimately connected to collapsed hyphal detritus of universal veil (see below); filamentous undifferentiated hyphae 1.0–5.0  $\mu\text{m}$  wide, branching, dominating, subradially oriented, densely packed vertically, sometimes with hyphal tips expanded slightly at apex; vascular hyphae 1.4–7.1  $\mu\text{m}$  wide, common, sinuous, infrequently branching, without dominant orientation. PILEUS CONTEXT: filamentous undifferentiated hyphae 0.9–8.5  $\mu\text{m}$  wide, plentiful, branching, frequently fasciculate, forming matrix loosely to densely interwoven around acrophysalides; acrophysalides of two forms, away from stipe apex plentiful narrowly clavate to elongate (e.g.,  $152 \times 28$   $\mu\text{m}$ ,  $95 \times 42$   $\mu\text{m}$ ), above stipe apex dominating and densely packed with longitudinal orientation like stipe context acrophysalides and ovoid to elongate ovoid to subpyriform (up to  $74 \times 46$   $\mu\text{m}$  or larger), in umbo greatly reduced in number; vascular hyphae 2.5–17.8  $\mu\text{m}$  wide, branching (especially frequently in region above stipe in disc), sinuous to looping and interweaving in loose “knots,” common locally, especially common near pileipellis and in region above stipe in disc; clamps plentiful. LAMELLA TRAMA: bilateral, divergent;  $w_{\text{cs}} = 25\text{--}45$   $\mu\text{m}$ ; subhymenial base dominated by curved intercalary inflated cells (up to  $94 \times 22$   $\mu\text{m}$ ) sometimes as concatenated pair (together up to 111  $\mu\text{m}$  long) and then arising from filamentous undifferentiated hyphae arising in central stratum, otherwise arising from short partially inflated clavate segment in manner of chained pair, giving rise to cells of subhymenium; central stratum containing intercalary narrowly fusiform cells (e.g.,  $62 \times 14.0$   $\mu\text{m}$ ); filamentous undifferentiated hyphae 3.2–4.9  $\mu\text{m}$  wide, with those in subhymenial base sometimes giving rise to cells of subhymenium; vascular hyphae 2.0–11.3  $\mu\text{m}$  wide, occasionally branching, often sinuous, uncommon to locally common; clamps common in central stratum. SUBHYMENIUM:  $w_{\text{st-near}} = 105\text{--}130$   $\mu\text{m}$  (crushed?);  $w_{\text{st-near}} = 95\text{--}105$  (very good rehydration, estimated from measurement and partially schematic drawing);  $w_{\text{st-far}} = 150$   $\mu\text{m}$  (crushed?);  $w_{\text{st-far}} = 100\text{--}115$   $\mu\text{m}$  (very good rehydration, estimated from measured data and schematic drawing); cellular (pseudoparenchymatous) or dominated by inflated cells, with cells in 2 to 3 layers (1 to 2 layers below longest basidia), with some uninflated branched or unbranched elements arising from inflated cells of subhymenium and giving rise in turn to basidia/oles, otherwise with basidia arising from inflated cells up to  $12.0 \times 10.0$   $\mu\text{m}$ . BASIDIA: 29–56 (–59)  $\times$  (8.1–) 8.5–13.0  $\mu\text{m}$ , dominantly 4-sterigmate, rarely 5-sterigmate in immature material, with sterigmata up to  $5.5 \times 2.0$   $\mu\text{m}$ ; clamps and proliferated clamps plentiful, prominent. UNIVERSAL VEIL: *On pileus*: at least in moist conditions persisting to maturity in thin layer (25–45  $\mu\text{m}$  thick) and sometimes

giving hoary appearance to pileus, at 1250× in cross-section giving appearance of somewhat sparse “curly hair”; filamentous undifferentiated hyphae dominant, collapsed, partially gelatinized, mostly under 2.0 µm wide, curling or coiling, branching, without dominant horizontal orientation; inflated cells very infrequent, soon collapsed and gelatinized; vascular hyphae without dominant orientation, of width similar to other hyphae, moderately frequent, scattered. *On stipe base, exterior surface*: partially gelatinized, in a relatively shallow layer, interior visible through occasional gaps; filamentous undifferentiated hyphae 1.7–4.2 µm wide, in fascicles up to 12 or more hyphae wide or singly, densely criss-crossed and interwoven, with many larger fascicles longitudinally oriented, with occasional openings giving (on whole) appearance of openings in expanded net shopping bag. *On stipe base, interior*: rather dense lattice-like structure of plentiful interwoven filamentous undifferentiated hyphae, enclosing globose to ellipsoid to clavate cells (up to 66 × 38 µm), with such cells plentiful to locally dominating in regions somewhat distant from exterior surface layer, enclosing smaller less frequent often clavate cells near exterior surface layer. *On stipe base, inner surface*: like interior but broken and gelatinized, indicating gelatinization takes place within universal veil or at interface between universal veil and pileipellis. *STIPE CONTEXT*: longitudinally acrophysalidic; filamentous undifferentiated hyphae 2.0–7.0 µm wide, branching, rather common away from surface, becoming dominant and strongly longitudinally oriented toward outer surface, at which forming dense pellis-like layer; acrophysalides up to 182 × 24 µm, smaller near exterior surface, with walls thin or up to 0.7 µm thick, with some near surface having yellowish walls; vascular hyphae 2.1–10.1 µm wide, sometimes sinuous, infrequent, unevenly distributed. *PARTIAL VEIL*: underside strongly gelatinized; upper side bearing plentiful remnants of inflated cells from former interface to lamellae edges; filamentous undifferentiated hyphae 1.5–4.5 µm wide, branching, dominant in interior, dominantly subradially oriented, dominantly fasciculate (with fascicles mostly 4 to 5 hyphae wide); inflated cells of interior common, clavate, to elongate ellipsoid, thin-walled, up to 28 × 17.5 µm, terminal, solitary, often with subradial orientation of longer axis, unevenly distributed, occasionally in small clusters; vascular hyphae not observed. *LAMELLA EDGE TISSUE*: sterile.

*BASIDIOSPORES*: [558/27/16] (7.5–) 8.0–11.0 (–13.6) × (5.7–) 6.5–8.4 (–9.9) µm, (**L** = (8.3–) 8.7–10.0 (–10.3) µm; **L'** = 9.4 µm; **W** = (6.6–) 6.9–7.7 (–7.8) µm; **W'** = 7.3 µm; **Q** = (1.06–) 1.15–1.43 (–1.73); **Q** = (1.22–) 1.24–1.37 (–1.40); **Q'** = 1.29), hyaline, colorless, thin-walled, smooth, inamyloid, broadly ellipsoid to ellipsoid, rarely elongate, usually at least somewhat adaxially flattened, wand-like or very narrowly clavate in early development;

apiculus sublateral (or rarely lateral in immature material), cylindric; contents monoguttulate to multiguttulate, with or without small additional granules; white in deposit.

ECOLOGY: Costa Rica: Solitary to subgregarious, at 1000–2500 m elev. In mixed forest with, and sometimes dominated by, *Quercus* (including *Q. brenesii*, *Q. copeyensis*, *Q. oocarpa*, and *Q. seemannii*), with or without substantial understory. Honduras: In undisturbed *Quercus* forest.

MATERIAL EXAMINED: COSTA RICA: ALAJUELA—Bosque del Niño, 31.v.1996 R.E. Halling & J.L. Mata [Halling 7591] (NY; USJ). CARTAGO—Estrella, 28.vii.1992 B.A. Strack & G.M. Mueller [Mueller 4433] (F 1102486), 4.vi.1996 R.E. Halling & J. Ammirati [Halling 7603] (NY; USJ); Tapanti, 20.vi.2001 R.E. Halling & J. Carranza [Halling 8198] (NY; USJ). GUANACASTE—Cacao no. 2, 4.vi.1994 J.P. Schmit 475 (F; USJ). SAN JOSÉ—La Chonta, 11.vii.1982 L.D. Gómez 18172 (F 1100529), 7.vi.1994 R.E. Halling & T.J. Baroni [Halling 7237] (NY; USJ), 16.vi.1995 K. Shanks, R.E. Halling, R.E. Tulloss & R.H. Petersen [Tulloss 6-16-95-C] (RET 333-6; USJ), R.E. Tulloss 6-16-95-D (RET 332-7; USJ), R.E. Halling s.n. [Tulloss 6-16-95-K] (RET 337-1; USJ), 11.vi.2001 R.E. Halling, B. Buyck, R. Aldana-Gómez [Halling 8178] (NY; USJ); El Empalme, 15.vi.1995 R.E. Halling, R.H. Petersen, K. Shanks, R.E. Tulloss [Tulloss 6-15-95-H] (RET 333-2; USJ); Jardín de Dota, 13.vii.1993 G.M. Mueller 4501 (F 1110801); San Gerardo de Dota no. 1, 8.vi.1994 R.E. Halling s.n. [G.M. Mueller 4659] (F 1112080; USJ), 21.vi.1995 R.E. Tulloss 6-21-95-G (holotype, USJ; isotype, NY), 24.vi.1997 R.E. Halling, G.M. Mueller, S. Huhndorf & D. Quist [Halling 7737] (NY; USJ). HONDURAS: FRANCISCO MORAZAN—Tegucigalpa – P. N. La Tigre, Sendero Bosque Nublado, 4.vii.1991 G.M. Mueller, B.A. Strack, R. & M. Singer & R. Andino [Mueller 4119] (F 1098650).

COMMENTS — The (a) relatively shallow subhymenium; (b) subhymenial base dominated by elongate, curved, intercalary cells; (c) plentiful clamps at bases of basidia; (d) habit; (e) proportionately long marginal striations; (f) strongly pigmented pileus and stipe decoration; and (g) broadly ellipsoid to ellipsoid spores indicate that this entity has strong affinity to the group of taxa phenetically similar to *A. hemibapha* (Berk. & Broome) Sacc. (Saccardo 1887), *A. jacksonii* Pomerl. (Pomerleau 1984), *A. arkansana* H.R. Rosen (Rosen 1926), *A. hayalyuy* Arora & Shepard (Shepard et al. 2008), etc.—taxa of *Amanita* stirps *Hemibapha* (Tulloss 1998a, 2009a).

The species of the above cited group that is most similar to *A. garabitoana* in habit and in size and shape of spores is *A. arkansana* the known range of which lies within the southeastern United States (Arkansas to the Gulf Coast states—from Texas to Florida). The present taxon differs from *A. arkansana* in at least the following:

- Pigmentation: The North American species lacks olivaceous tints in the pileus at all stages of development and is not as deeply pigmented as is

the red-brown disc of *A. garabitoana*; moreover, *A. arkansana* retains its yellow-orange coloration as dried rather than becoming dark brown to sordid or olivaceous tan. In addition, the patches on the stipe of *A. arkansana* are concolorous with the stipe (yellow) at first and become deeper yellow or more orange from handling; they are never olivaceous or sordid yellow.

- Fragile outer part of pileus: The basidiome of *A. arkansana* is notoriously fragile and difficult to collect without breaking, which is not the case for *A. garabitoana*. The portion of pileus context with greater thickness than a membrane extends half or less of the radius toward the margin in examined material of *A. arkansana*, but 75% to 85% of the radius in *A. garabitoana*.
- Fragility of the stipe: The ratio of the diameter of the central cylinder to the diameter of the stipe (both measured at midstipe) in specimens of the two taxa are 0.5–0.56 for *A. arkansana* and 0.21–0.42 (–0.52) for *A. garabitoana*. Hence, the context forms a supporting wall with thickness of 22%–25% of the stipe diameter in the northern species and with (24%–) 29%–40% of the stipe diameter in the mesoamerican species.
- Tyrosinase spot test: In contrast to the strong positive reaction for tyrosinase in *A. garabitoana*, that reaction is very limited in most of the context of *A. arkansana*. In immature material of *A. arkansana*, using paracresol, a positive reaction for tyrosinase was only seen in the limb of the volva and in five, small and widely scattered spots on the stipe and pileus context after 18 min. Another test with more mature material, using L-tyrosine (only on pileipellis, stipe surface, and stipe context), produced very faint positive reaction on the stipe surface and pileipellis after 19 min. Voucher specimens: Tulloss 10-26-85-A and 7-16-87-C.
- Spore size: Spores of *A. arkansana* are somewhat smaller than those of *A. garabitoana*: [290/13/7] (7.0–) 7.7–10.5 (–15.0) × (5.6–) 6.0–8.0 (–10.2) μm, (L = (8.0–) 8.3–9.9 μm; L' = 9.0 μm; W = (6.3–) 6.5–7.3 μm; W' = 6.9 μm; Q = (1.10–) 1.19–1.43 (–1.70); Q = (1.22–) 1.24–1.38; Q' = 1.30).

MATERIAL EXAMINED (*Amanita arkansana*): U. S. A.: ARKANSAS—Pulaski Co. – Little Rock, Arkansas Dept. of Pollution Control & Ecology, 14.vi.1994 J. Justice s.n. (RET 136-6). Washington[?] Co. – E of Fayetteville, E of Mt. Sequoia, 13.x.1925 [packet marked “13.x.1926” (sic)] H.R. Rosen s.n. (holotype<sup>1</sup>, BPI; isotypes TENN 21294 & 21299). FLORIDA—Alachua Co. – Gainesville, across from Florida St. Mus., 11.viii.1985 A. Norarevian s.n. [Tulloss 8-11-85-AN1] (RET 137-5). MISSISSIPPI—Jackson Co. – Pascagoula R. Wildlife Mgt. Area, 16.viii.1987 D.C. & R.E. Tulloss 7-16-87-C (in herb. David T. Jenkins, Univ. Ala., Birmingham; RET 149-5). MISSOURI—Stoddard Co. – Mingo Nat. Wildlife

Refuge, 19.ix.2008 J. Justice s.n. (RET 450-8). TEXAS—Hardin or Tyler Co. — Big Thicket Nat. Preserve, Turkey Crk. Unit, 26.x.1985 A. Norarevian & J. Justice s.n. [Tulloss 10-26-85-A] (RET 139-10); Tyler Co. — 8 km E of Spurger, Forest Lake Exp. For., off rd. FM1013, ca. plots 39 & 41, 26.vi.1994 D.P. Lewis 5302 (RET 283-5).

So far as is known (C. Bas pers. corresp.; Tulloss unpub. data), it is not unusual to find vascular hyphae especially plentiful in the pileus context above the stipe in *Amanita*. This is an item worthy of further study. Bas (1969 and pers. corresp.) has noted that vascular hyphae are sometimes concentrated in damaged areas in *Amanita*. Since they arise from filamentous undifferentiated hyphae (Tulloss unpub. data), it may be the case that they are produced in response to damage or in areas of mechanical stress (such as the stipe-pileus convergence region). One hypothesis might be that the (partially?) insoluble material often seen when a vascular hypha is cut or broken during sectioning may include an antibiotic or some other aid to maintaining the integrity of the basidiome and, hence, reproduction of the species.

We also wish to make it clear that we make no claim for novelty with regard to the arrangement of acrophysalides in the center of the pileus. However, it does seem of interest to examine (in the future) the mechanical structure(s) by which the joining of the stipe and cap takes place in *Amanita*.

Mueller 4501 was immature when dried; in measuring spores from a single mount, three 5-sterigmate basidia were noted with the sterigmata bearing content-less, wand-like or very narrowly clavate spores. The single basidiome of this collection is considered by us to be bearing abnormal spores.

Mueller 4119 was immature when dried.

## 2. Section *Lepidella*

2.1. Key to section *Lepidella* in Costa Rica and Honduras — This key treats only those subsections of section *Lepidella* represented in the region of study. Species marked by an asterisk (\*) are not treated at length in this paper.

1. Pileus pinkish buff; universal veil on pileus in tightly appressed patches, white to concolorous, comprising outer layer of interwoven filamentous undifferentiated hyphae and interior dominated by chains of narrow, relatively large, inflated cells with periclinal orientation, pileipellis poorly developed; spores (7.8–) 8.2–10.0

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1. While there are three collections representing parts of the original collection, none is marked as the holotype. The place of deposit of the holotype was not provided in the protolog. BPI was indicated as the location of the “type” by Gilbert (1940-41: 98, caption for Tab. IX, fig. 2). This is fortunate because the portion of the type in BPI has the most thorough and abundant representation of all parts of the included basidiomes of any of the three duplicates of the original collection.

(-10.5)  $\times$  (5.5-) 6.0-7.0 (-8.0)  $\mu\text{m}$ , with  $Q = 1.34-1.39$  (*Amanita* subsect. *Vittadini* Bas) .....

*A. species* HON1\*.

1. Universal veil as warts or irregular patches or as pyramidal warts; elements comprising these warts disordered or having more or less anticlinal orientation, never as chains of relatively large, narrow, inflated cells with strong periclinal orientation.

2. Outer layer of volva consisting mainly of hyphae; consequently, often with small, incomplete volval limb on stipe's basal bulb; lamellae ochraceous to yellow to pale orange. (*Amanita* subsect. *Gymnopodae* Bas).....

3. Spores (7.8-) 8.1-10.0 (-11.5)  $\times$  (5.3-) 6.0-7.5 (-8.7)  $\mu\text{m}$ , with  $Q = 1.33-1.41$  (-1.44); found at 1600-1720 m elev. in Prov. Cartago with *Quercus oocarpa* and *Q. seemannii* .....

*A. conara*.

3. Spores (6.1-) 7.0-9.5 (-11.6)  $\times$  (5.1-) 6.9-7.9 (-9.5)  $\mu\text{m}$ , with  $Q = (1.11-)$  1.15-1.23; found at 1350-1500 m elev. in Prov. Puntarenas with *Q. corrugata* and *Q. seemannii* .....

*A. species* CR18\*.

2. Volva never submembranous, never forming limb at base of stipe; lamellae never ochraceous (*Amanita* subsect. *Solitariae* Bas).

4. Pileus rat gray to brown, micaceous gray to pallid in age or after rains wash away pigment, with brownish gray pulverulent universal veil remains in pyramidal warts or irregular patches, often darker than pileipellis; bulb of stipe napiform to radicating, often markedly radicating; spores (7.5-) 8.5-13.2 (-16.0)  $\times$  (5.1-) 6.0-8.5 (-12.6)  $\mu\text{m}$ , with  $Q = 1.35-1.68$  (-1.70) .....

*A. costaricensis*.

4. Pileus and universal veil white, at least at first.

5. Much of basidiome staining ochraceous buff to rust colored to chestnut brown or yellow to cinnamon; universal veil on pileus as flattened to slightly erumpent large warts or small patches; all parts of basidiome liable to staining pale yellowish and, eventually, cinnamon; bulb of stipe napiform, never abrupt or subabrupt, decorated with narrow rings of volval tissue beginning on lower stipe above bulb and continuing to approximately broadest part of bulb; spores (8.5-) 9.0-12.5 (-14.0)  $\times$  (6.5-) 7.0-9.5 (-10.2)  $\mu\text{m}$ , with  $Q = 1.29-1.32$  .....

*A. advena*\*.

5. Pileus not staining, often covered rather densely by minute pyramidal warts; bulb slenderly subnapiform to napiform, subradicating, with either rings of flocculence or minute pyramidal warts around top of bulb; spores (7.0-) 9.1-13.0 (-17.5)  $\times$  (5.2-) 5.9-7.8 (-9.5)  $\mu\text{m}$ , with  $Q = (1.35-)$  1.50-1.81 .....

*A. polypyraxis*\*.

## 2.2. Descriptions of taxa —

*Amanita conara* Tulloss & Halling **sp. nov.**

FIGS. 5–8

MYCOBANK MB 518296

*Pileus* 60–150 mm *latus*, *subochraceobubalinus* vel *subbubalinus* vel *aurantiocremeus* vel *griseaurantius*, *labibus* *subaurantiis* vel *subbrunneis*, *marginem* *longistriato*, *nonappendiculato*, *reliquiis* *veli universalis verrucas* vel *assumenta formanti*. *Lamellae liberae*, *subconfertae* vel *confertae*, *subcremeae* vel *subaurantio-flavobubalinae*; *lamellulae subattenuatae* vel *rotundato-truncatae* vel *truncatae*. *Stipes* 71–115<sup>+</sup> × 11–30<sup>±</sup> mm, *albus* vel *subroseus* vel *subbrunneoroseus*, *annulatus*, *bulbo robusto* 42–60 × 37–60 mm, *interdum velo universali membranaceo pertenui super bulbum*. *Basidiosporae* (7.8–) 8.1–10.0 (–11.5) × (5.3–) 6.0–7.5 (–8.7)  $\mu\text{m}$ , (*L* = (8.6–) 8.8–9.4  $\mu\text{m}$ ; *L'* = 9.1  $\mu\text{m}$ ; *W* = 6.5–6.8 (–7.0)  $\mu\text{m}$ ; *W'* = 6.6  $\mu\text{m}$ ; *Q* = (1.17–) 1.23–1.51 (–1.70); *Q* = 1.33–1.41 (–1.44); *Q'* = 1.37), *amyloideae*, *late ellipsoideae* vel *ellipsoideae*. *Basidia* 30–58 × 9.1–13  $\mu\text{m}$ . *Fibulae relative communis*. *In quercetis tropicalibus montanis costaricensibus habitat*. *Species Amanitae subsectionis Gymnopodae simulanissima*. *Species nova ob distributionem geographicam, magnitudinem et formam sporarum, consortionem Quercu, colorem et formam et anatomiam microscopicam veli universalis et limbi interni, et absentiam rhizoidei bulbo stipitis*.

**HOLOTYPE** — Costa Rica, Prov. Cartago, Estrella, 14.vi.1996 R.E. Halling & J. Ammirati [Halling 7686] (USJ).

**ETYMOLOGY** — *kovapoc* (Grk.), fat or well-fed, because of the large basal bulb of the present species; proposed English name, “Fat Barefoot Lepidella.”

**PILEUS:** 60–150 mm wide, light ochraceous buff (ca. 5A2) with light orange stains (ca. 6A4) or pale buff to faintly tannish or orangish cream (paler and more tan than 7.5YR 8/4, paler than 10YR 8/4) or grayish orange (6B4), occasionally stained faintly brown here or there, convex at first, planoconvex and somewhat undulate at maturity, not viscid when wet, dull at first, later shiny when dry; *context* white to cream to slightly brownish cream, context unchanging or slowly staining brown to reddish brown when cut or bruised, 7–15 mm thick at stipe, thinning evenly and slowly to margin, rather thick even near margin; *margin* nonstriate, decurved, appendiculate (at first with appendiculate material floccose and pale pinkish, at maturity only with scattered crumb-like bits); *universal veil* as crumb-like warts or pyramidal warts over disc, sometimes as eccentric patches, at first pale orangish white to pinkish (5A2, paler toward pileus margin) becoming sordid or brown or taking on brownish tint, smooth surfaced, often easily taking fingerprint, pulverulent to subfelted, deterrent, with patches having membranous upper layer.

**LAMELLAE:** free, with decurrent lines on stipe apex connecting to striations on upper surface of partial veil, close to subcrowded to crowded, pale cream (immature) to slightly orangish yellowish tan in mass, more vividly colored in



Fig. 5. *Amanita conara*. Habit (Halling 7272) ( $\times 0.45$ ). Photo by R. E. Halling.

side view [light cream in immature material, then more yellow than 2.5Y 7/6 or more brown than 2.5Y 8/6 or more orange than 4B6 or more brown than 4A6 or pale yellow (4A4) or pale orange (5A3)], unchanging when cut or bruised, 6.5–12 mm broad, occasionally forked, with edge minutely pulverulent and white to approximately concolorous with partial veil; *lamellulae* subattenuate to rounded attenuate to truncate, unevenly distributed, of diverse lengths, plentiful.

**STIPE:** 71–115<sup>+</sup>  $\times$  11–30<sup>±</sup> mm, white, sometimes with ochraceous to light orange stains, sometimes faintly brick colored or pale pink after handling or in wounds, narrowing upward, flaring at apex, pulverulent above partial veil, sometimes satiny below partial veil, longitudinally striatulate, with upward pointing fibrillose scales or squamules [concolorous to light orange (ca. 6A4), with tips sometimes faintly brick colored or concolorous with partial veil and limbus internus of universal veil], with shaggy region beginning below annulus and ending roughly 10 mm above bulb; *bulb* 42–60  $\times$  37–60 mm, robustly clavate-subnapiform to robustly napiform, with white mycelial threads prominent at very base; *context* solid or stuffed? (possibly appearing so due to larval damage), concolorous with pileus context, with bruising/staining reaction as in pileus context, with larval tunnels yellowish in center of stipe and reddish brown elsewhere; *partial veil* apical, submembranous, shredding, sometimes deciduous at least in part, pale orangish white (5A2), with underside bearing



Fig. 6. *Amanita conara*. Habit (Tulloss 6-13-95-C) ( $\times 0.74$ ). Photo by R.E. Tulloss.

warts and flocculence, with upper side striate, sometimes thickened at edge; *universal veil* often present as short thin limb and/or in incomplete and sometimes slightly overlapping rows of triangular flaps (minute, weakly structured, upward-pointing)  $0.5 \pm$  mm high on (or appressed to) upper part of bulb, with edges of such structures sometimes appearing frayed and darkening with age (viewed at  $6-12\times$ ), often with nearly complete limbus internus partially encircling (about half-circumference) base of stipe and in other small fragments on lower stipe above bulb, 1–2 mm thick, nearly white to pale orangish white (5A2).

*Odor* “earthy” in immature specimen; rich, strong, like “old ham” (but sometimes not unpleasantly) or like “unwashed athletic socks” in mature material. *Taste* not recorded.

**MACROCHEMICAL TESTS:** Spot test for laccase (syringaldazine): negative throughout basidiome. Spot test for tyrosinase (paracresol): positive in stipe (excluding bulb) and pileipellis and often in large areas of lamellae and pileus context (outside of disc) or strongly positive throughout basidiome except for parts of lamellae. Test vouchers: Halling 7272, Mueller 4643, Tulloss 6-13-95-C.

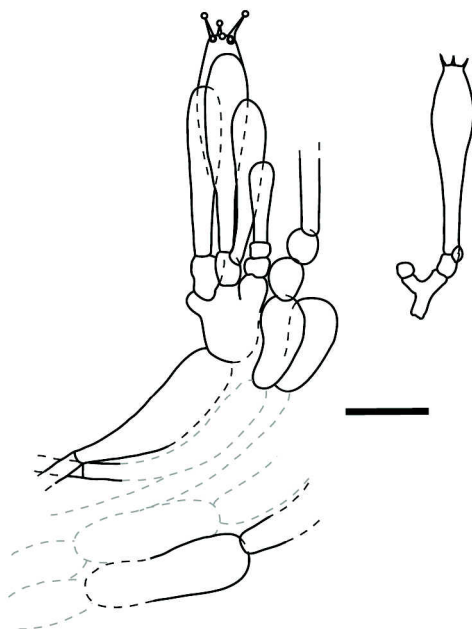


Fig. 7. *Amanita conara* (holotype). Elements of hymenium and subhymenial tree (gray lines of subhymenial base are semischematic). Scale bars = 20  $\mu$ m.

**PILEIPELLIS:** narrow and with pronounced boundaries, bounded above by densely placed anticlinally oriented hyphae binding upper surface to remains of universal veil, bounded below by loosely interwoven and disordered tissue of pileus context, with separation from universal veil at first via mechanical rupture of hyphae; 30–55  $\mu$ m thick at approximately midradius in mature or near mature material, lacking substantial suprapellis, with gelatinization absent even at point of breaking of partial veil and in mature material limited to surface, with elements densely packed vertically, yellow-orange; filamentous undifferentiated hyphae 2.5–7.5  $\mu$ m wide, branching, disordered and interwoven over disc, dominantly subradially arranged with some criss-crossing hyphae away from disc, often yellow or yellowish, hyphal tips of broader hyphae common; vascular hyphae 3.4–11.4  $\mu$ m wide, sinuous, sometimes in tangles, yellow, scattered. **PILEUS CONTEXT:** filamentous undifferentiated hyphae 2.5–8.9  $\mu$ m wide, occasionally branching, sometimes fasciculate, common in disc, plentiful at mid-radius; acrophysalides broadly ellipsoid to ellipsoid (up to 80  $\times$  60  $\mu$ m in disc) or clavate (up to 131  $\times$  48  $\mu$ m), similarly shaped and smaller at mid-radius, commonly with inflated subterminal cell, in disc dominating and disordered, at mid-radius plentiful and with tendency to

subradial orientation; vascular hyphae 2.8–17.8  $\mu\text{m}$  wide, sinuate to hypersinuate, rarely branching, common in region immediately below pileipellis, rather common elsewhere, scattered in all mounts. LAMELLA TRAMA: bilateral, divergent;  $w_{\text{cs}} = 50\text{--}65$   $\mu\text{m}$  (good rehydration); central stratum comprising interwoven filamentous undifferentiated hyphae 2.5–11.4  $\mu\text{m}$  wide, lacking inflated intercalary segments; subhymenial base dominated by densely packed divergent filamentous undifferentiated hyphae 3.8–11.4  $\mu\text{m}$  wide, with angle of divergence shallow; terminal, inflated cells not observed; vascular hyphae 2.3–8.5  $\mu\text{m}$ , infrequently branching, sinuous, uncommon. SUBHYMENIUM:  $w_{\text{st-near}} = 70\text{--}85$   $\mu\text{m}$  (moderate to good rehydration);  $w_{\text{st-far}} = (80\text{--}) 90\text{--}105$   $\mu\text{m}$  (moderate to good rehydration); scant, often with only one (or no) cell(s) between bases of longest basidia/-oles and subhymenial base, with basidia arising from elongate cells of subhymenial base and subglobose to branched to ellipsoid to clavate cells and uninflated hyphal segments, with such elements arranged approximately perpendicular to central stratum. BASIDIA: (30–) 34–59 (–60)  $\times$  9.1–13.0 (–14.4)  $\mu\text{m}$ , 4-sterigmate, with sterigmata up to 7.5  $\times$  2.0  $\mu\text{m}$  and sometimes subcylindric; clamps and proliferated clamps relatively common. UNIVERSAL VEIL: *On pileus, exterior surface*: particularly well-formed and in place on surface of patches, very thin, comprising lattice of irregularly ordered fascicles of partially gelatinized orange-brown hyphae, with fascicles up to 18 (or more) hyphal diameters wide; filamentous undifferentiated hyphae 1.8–3.9  $\mu\text{m}$  wide, branching; with immediately underlying thin membranous layer, comprising loosely interwoven filamentous undifferentiated hyphae 2.2–8.9  $\mu\text{m}$  wide, disordered, commonly branching, anastomosing, plentiful to dominating, sometimes in narrow fascicles, thin-walled, colorless and hyaline to (infrequently) yellowish and subrefractive; inflated cells uncommon, terminal, singly or in pairs, broadly clavate to clavate to cylindric, thin-walled, hyaline, up to 57  $\times$  13.0  $\mu\text{m}$ ; vascular hyphae not observed. *On pileus, interior*: all elements strongly vertically aligned, orange-brown on wart surface; filamentous undifferentiated hyphae 1.0–12.1  $\mu\text{m}$  wide, frequently branching, occasionally anastomosing, inside wart colorless and hyaline or (occasionally) yellowish and with subrefractive walls; inflated cells in terminal chains of up to at least five, thin-walled, plentiful, colorless and hyaline inside wart, barrel-shaped to ovoid to broadly clavate to clavate to narrowly fusiform and up to 48  $\times$  25  $\mu\text{m}$  in lower third of wart above basal part and subglobose to ellipsoid to clavate (up to at least 78  $\times$  38  $\mu\text{m}$ ) to narrowly clavate or narrowly fusiform (up to 91  $\times$  19.0  $\mu\text{m}$ ) to irregularly shaped and sometimes connected with three or more hyphae via separate septa in upper third of wart; vascular hyphae not observed except in upper part of wart and there very infrequent and (e.g.) 2.2–4.9  $\mu\text{m}$  wide. *On pileus, basal part*:

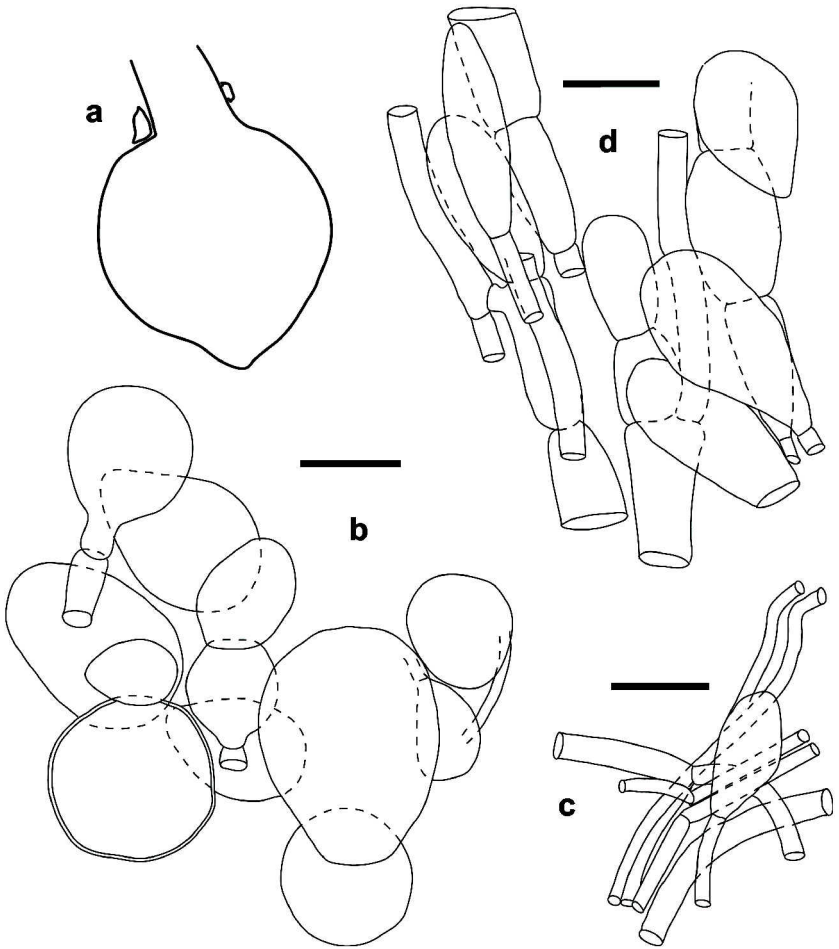


Fig. 8. *Amanita conara*. a. Cross-section of fragments of limbus internus on bulb and lower stipe (Tulloss 6-13-95-C) ( $\times 0.82$ ). b. Elements of universal veil (limbus internus) viewed through—from above—remains of partial veil (not shown) (holotype). c. Elements of universal veil, just below gelatinized hyphal layer on top of pileal wart (Halling 7272). d. Elements of universal veil near base of pileal wart (Halling 7272). Scale bars = 20  $\mu\text{m}$ .

densely packed, anticlinally aligned hyphae connecting intimately with pileipellis. *On underside of partial veil* (i.e., limbus internus): filamentous undifferentiated hyphae 2.2–10.8  $\mu\text{m}$  wide, occasionally branching, common; inflated cells dominating, terminal singly or as concatenated pairs, globose to subglobose to pyriform to broadly ellipsoid to ellipsoid to elongate to broadly

clavate to clavate to narrowly clavate (up to  $60 \times 33 \mu\text{m}$ ), dominantly thin-walled, occasionally with wall up to  $0.8 \mu\text{m}$  thick; vascular hyphae not observed. *On stipe base*: with structure very like that of surface layers of universal veil on pileus; filamentous undifferentiated hyphae dominating, thin-walled, slightly gelatinized at surface, hyaline and colorless or (occasionally) with walls yellowish and subrefractive,  $2.5\text{--}10.0 \mu\text{m}$  wide, commonly branching, fasciculate, densely packed, with predominantly vertical orientation (i.e., not disordered as on pileus); inflated cells rather infrequent, scattered, terminal, narrowly clavate to clavate (e.g.,  $30^+ \times 12.5 \mu\text{m}$ ); vascular hyphae not observed; clamps not observed. *STIPE CONTEXT*: longitudinally acrophysalidic; filamentous undifferentiated hyphae  $3.2\text{--}17.8 \mu\text{m}$  wide, branching occasionally, plentiful in interior, dominant near surface, sometimes constricted at septa; acrophysalides up to at least  $395 \times 32 \mu\text{m}$ , plentiful in interior, common near surface; vascular hyphae  $7.6\text{--}11.4 \mu\text{m}$  wide, sinuous, infrequent, occasionally clustered; clamps not observed. *PARTIAL VEIL*: very thin and sparse layer of criss-crossing, hyphae, in mounts dominated by inflated cells of limbus internus attached to underside of hyphal framework; filamentous undifferentiated hyphae  $1.5\text{--}3.8 \mu\text{m}$  wide, occasionally branching, in narrow fascicles, rapidly gelatinizing prior to maturity of basidiome; inflated cells not observed; vascular hyphae not observed. *LAMELLA EDGE TISSUE*: sterile.

*BASIDIOSPORES*:  $[181/8/4] (7.8\text{--}) 8.1\text{--}10.0 (-11.5) \times (5.3\text{--}) 6.0\text{--}7.5 (-8.7) \mu\text{m}$ , ( $L = (8.6\text{--}) 8.8\text{--}9.4 \mu\text{m}$ ;  $L' = 9.1 \mu\text{m}$ ;  $W = 6.5\text{--}6.8 (-7.0) \mu\text{m}$ ;  $W' = 6.6 \mu\text{m}$ ;  $Q = (1.17\text{--}) 1.23\text{--}1.51 (-1.70)$ ;  $Q = 1.33\text{--}1.41 (-1.44)$ ;  $Q' = 1.37$ ), hyaline, colorless, thin-walled, smooth, amyloid, broadly ellipsoid to ellipsoid, sometimes swollen at one end, often at least somewhat adaxially flattened; apiculus sublateral, cylindric; contents multi- to monoguttulate; color in deposit unknown.

*ECOLOGY*: Subgregarious to scattered, at 1600–1720 m elev. In thick, dark, wet loam under shallow layer of leaf litter of mixed broadleaf forest including *Quercus oocarpa* or in such a habitat with that tree and *Q. seemannii*.

*MATERIAL EXAMINED*: COSTA RICA: CARTAGO—Estrella, 14.vi.1996 R.E. Halling & J. Ammirati [Halling 7686] (holotype, USJ; isotype, NY); off Interamerican Hwy., 6 km S of Cartago at rd. to Palo Verde, 28.vii.1992 B.A. Strack & G.M. Mueller [Mueller 4434] (F 1102487); Palo Verde, 31.v.1994 G.M. Mueller 4643 (F 1112041; USJ), 11.vi.1994 R.E. Halling & T.J. Baroni [Halling 7272] (NY; USJ), 13.vi.1995 R.E. Tulloss 6-13-95-C (RET 153-4; USJ).

*COMMENTS* — Four taxa have been assigned to *Amanita* subsect. *Gymnopodae* world wide, but all can be easily distinguished from the present species. In addition to their general habit, three of these species have in common with *A. conara* a number of distinctive characters among which are rubescent or dark-

ening context, a distinctive odor, yellow or orange tints on the lamellae, and a submembranous surface layer of the universal veil.

- *Amanita gymnopus* Corner & Bas (Corner & Bas 1962), described from Malaysian “jungle” and reported from southern China (Chen et al. 2001, Yang 2005) and Japan (Hongo 1982), has small ( $5-7 \times 5-6.5 \mu\text{m}$  per Corner and Bas), globose to subglobose spores; a universal veil that forms submembranous patches and not warts on the pileus; and marked rhizoids attached to the stipe base (Bas 1969: fig. 378). Chen et al. reported spores of  $6.0-7.5 (-8.0) \times (5.0-) 5.5-6.5 \mu\text{m}$  from a single specimen. Yang reported spore data as follows in specimens from at least three localities:  $6.0-8.5 \times (5.0-) 5.5-7.5 \mu\text{m}$ , ( $Q = (1.03-) 1.07-1.24 (-1.42)$ ;  $Q = 1.14 \pm 0.08$ ).<sup>1</sup>
- *Amanita ochraceobulbosa* A. E. Wood (Wood 1997) has subglobose to broadly ellipsoid spores  $9.3-11.7 \times (7.3-) 8.1-9.6 (-10.2) \mu\text{m}$  with est.  $Q = 1.2$ , a cap that is cream to cream-buff to yellow-orange-cream with universal veil remains as (often large) pyramidal warts, gills that are white to cream, flesh that apparently is nonstaining when cut or bruised, and pyramidal warts sometimes present on the stipe’s basal bulb. Absence of a submembranous outer volval layer, presence of warts on the bulb, and no mention of staining flesh or distinctive odor suggest that this taxon is not appropriately placed in subsect. *Gymnopodae*.
- *Amanita ochrophylla* (Cooke & Massee) Cleland (Cleland 1924), described from edges of open forest in eastern and southeastern Australia (Bas 1969: 556), has larger, proportionately narrower spores ( $9-11 \times 5.5-7 \mu\text{m}$ ) with  $Q = 1.3-2.0$  and  $Q = 1.5-1.8$ ; a limbus internus that is apparently more coherent than that of *A. conara* and is frequently left as a “second annulus” on the stipe just below the partial veil (Bas 1969: fig. 374); flesh that becomes pink on exposure; etc. Wood (1997: 803) gives spore measurements as follows:  $9.3-10.8 (-12.6) \times 5.4-7.4 (-8.4) \mu\text{m}$ , with  $Q = 1.43-1.72 (-1.88)$ . We estimate  $Q'$  for Wood’s material as 1.55–1.6.
- *Amanita ochrophylloides* D. A. Reid (Reid 1978, 1980), described from “under *Eucalyptus* sp. (of peppermint group)” in the state of Victoria, Australia, has predominantly subglobose to broadly ellipsoid to ellipsoid spores ( $7.0-10.0 \times 5.0-8.0 \mu\text{m}$ , with est.  $Q = 1.3$ ); a pale brown pileus with dark, “strobiliform” warts; a tendency to darken from handling; pale golden yellow lamellae; a slight volval limb on the

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1. Yang’s  $Q$  corresponds to the  $Q$  of our notation; and his  $Q$ , to our  $Q'$ .

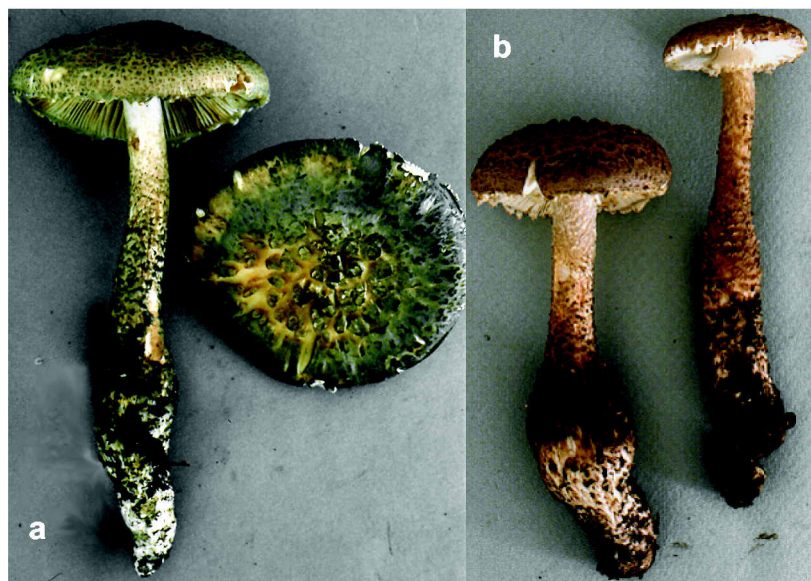


Fig. 9. *Amanita costaricensis*. a. Habit (holotype) with weathered cap on right ( $\times 0.55$ ). b. Habit (Tulloss 6-23-95-M) ( $\times 0.37$ ). Photos by R. E. Tulloss.

stipe's basal bulb; an odor that is faint and mealy; abundant, highly refractive hyphae in the universal veil on the pileus; etc.

Guzmán (1975) reported *A. ochrophylla* from *Quercus* forest in Guerrero. His macroscopic description fits *A. conara* rather well; and his measurements for spores are  $9-11 \times (5.5-6.0-7.5 \mu\text{m})$ . This is a relatively good match for our spore data from *A. conara*. We estimate a  $Q'$  of approximately 1.5 for spores of Guzmán's material. We have not yet reviewed the material Guzmán cited, but it appears to us that *A. conara* may occur in Mexico.

Mueller 4643 consists of a single, rather large, immature specimen of *A. conara*. It comes from the same habit as the other material cited and is easily recognizable because of excellent photographs and notes on fresh material that accompany the exsiccatum; moreover, the thin membranous outer layer of the universal veil can be seen on scalp sections of the universal veil remnants on the pileus.

We have three collections of what appears to be a similar, but possibly distinguishable, taxon from Ctn. Coto Brus, Prov. Puntarenas (La Amistad sites nos. 1 and 2) in association with *Q. corrugata*, *Q. seemannii*, and other oaks and belonging in subsection *Gymnopodae* ("species CR18" in the above key).

These collections differ from *A. conara* in colors of the basidiome (not all collections are fully annotated) and consistently have smaller subglobose to broadly ellipsoid spores: [160/8/3] (6.1–) 7.0–9.5 (–11.6)  $\times$  (5.1–) 5.9–7.9 (–9.5)  $\mu\text{m}$ , (**L** = 7.6–8.2 (–8.3)  $\mu\text{m}$ ; **L'** = 7.9  $\mu\text{m}$ ; **W** = (6.3–) 6.7–7.0  $\mu\text{m}$ ; **W'** = 6.7  $\mu\text{m}$ ; **Q** = (1.04–) 1.08–1.29 (–1.41); **Q** = (1.11–) 1.15–1.23; **Q'** = 1.17). All three collections are deposited in NY (Halling 7803, 8148, 8360).

The present species was previously called “*A. species* CR10” in drafts and keys circulated by Tulloss.

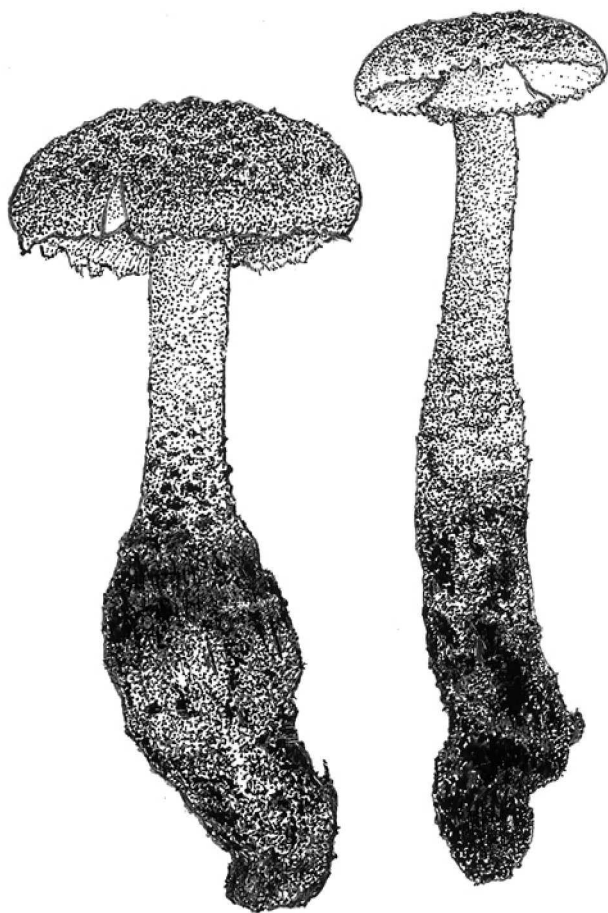
*Amanita costaricensis* Tulloss, Halling, G.M. Muell. & Singer **sp. nov.** FIGS. 9–11  
MYCOBANK MB 518297

*Pileus* (43–) 50–120 (–145) mm *latus*, *brunneus vel alutaceus vel griseus*, *aliquando subroseotinctus*, *disco fuscior*, *hemisphaericus vel convexus demum applanatus disco subumbonato*; *contexto albo*, *aliquando subochraceo ubi laeso*; *marginem appendiculato aliquando brevistriato*; *velo universali griseo vel brunneo vel atrobrunneo verrucato*. *Lamellae liberae vel subadnatae, confertae, saepe subventricosae*, 3–7.5 mm *latae, lamellis truncatis vel attenuatis*. *Stipes* 52–124  $\times$  9–18 (–22) mm, *subalbus vel griseus, annulatus, pulverulentus vel flocculosus sub annulo*; *bulbo* (30–) 57–112+  $\times$  17–40 mm, *napiformi vel dauciformi, radicanti*; *velo universali pulverulento vel verrucato, fuligineogriseo vel concoloro*. *Sporae amyloideae*, (7.5–) 8.5–13.2 (–16.0)  $\times$  (5.1–) 6.0–8.5 (–12.6)  $\mu\text{m}$ , (**L** = (9.1–) 9.4–12.3  $\mu\text{m}$ ; **L'** = 10.8  $\mu\text{m}$ ; **W** = 6.4–7.7 (–8.3)  $\mu\text{m}$ ; **W'** = 7.2  $\mu\text{m}$ ; **Q** = (1.10–) 1.27–1.83 (–2.15); **Q** = 1.35–1.68 (–1.70); **Q'** = 1.51), *late ellipsoideae vel ellipsoideae vel elongatae*. *Fibulae vulgaris*. *In quercetis tropicalibus montanis costaricensibus et hondurensibus habitat. Amanita onusta et A. atkinsoniana Amanitae stirpis Microlepis simulanissimae. Species nova ob magnitudinem sporarum, magnitudinem basidiomae, lamellarum non flavescentem et non celeriter putrescentem, et ubi probata paracresolo non reagens.*

**HOLOTYPE** — Costa Rica, Prov. San José, Ctn. Dota, 21.vi.1995 R.E. Halling s.n. [Tulloss 6-21-95-M] (USJ).

**ETYMOLOGY** — In honor of the Republic of Costa Rica.

**PILEUS:** (43–) 50–120 mm wide [up to 145 mm in Mueller 4368], brown (6C4–5) to light brown (5–6D4–5) to light brown with slight pinkish cast (ca. 7D5) to pale sordid tan to yellowish cream (then with sordid tan disc) to light brownish gray (7.0YR 5.4/1.2) to brownish gray to mouse (or rat) gray, micaceous gray in old material (Gómez & Alfaro 20641) or dull dark brown over disc [Mueller 4368], with pigment at least sometimes washed out by rain, hemispheric to convex at first, becoming applanate around subumbonate disc, tacky when moist, sometimes viscid over disc, dull to satiny to subshiny, shiny in age, sometimes becoming areolate and then with areolae centered on warts; *context* white, usually with pale brownish gray to gray to brown region under pileipellis, sometimes pale ochraceous when exposed, 3–10.5 mm thick over stipe, thinning evenly to margin; *margin* nonstriate, sometimes short sul-



D.C. Tulloss del.

Fig. 10. *Amanita costaricensis*. Habit (Tulloss 6-23-95-M) ( $\times 0.63$ ).

cate (0.05R) in age, incurved at first, then decurved, occasionally uplifted in age, appendiculate with white and or gray floccose-felted shreds of partial veil; *universal veil* as patches or flakes or warts (some rather broad and irregular, some small and pyramidal), often squamulose near margin, gray to brownish gray to brown or dark grayish brown and darker than pileus (6D-E4-6 to 7E6 to 7F7 to 5.6YR 3.4/0.9), occasionally as flat pinkish brown (7B4) patches, pulverulent, darkening with age, verruculose ( $10\times$  lens), destile.

LAMELLAE: free to narrowly adnate, close to subcrowded to crowded, lacking decurrent lines on stipe apex, white to pale cream in mass, off-white to slightly sordid white to very pale yellowish white in side view, reddish brown where damaged, relatively thick, 3–7.5 mm broad, frequently subventricose, entire, with thin gray edge; *lamellulae* truncate to rounded truncate to subattenuate to attenuate to attenuate in steps, plentiful, unevenly distributed, of diverse lengths or all very short [only reported for Mueller 4368].

STIPE: 52–124 × 9–18 (–22) mm [broadest in luxuriant mature specimen of Mueller 4368], ground color white to off-white to pale grayish, pallid to gray matte to whitish-gray and smooth to subglabrous above partial veil, below partial veil (and extending downward to first row of warts of universal veil) decorated with densely pulverulent to floccose or floccose-fibrillose universal veil (q.v.), with such material mouse gray to light gray-brown (ca. 7C3), later decorated with light gray-brown (5B3 to 9.7YR 6.4/2.5) granules and light gray-brown to reddish brown fibrillose upward pointing scales, with such material evenly distributed or in narrow concentric bands, finely striatulate with some raised fibrils in undecorated areas below partial veil, with surface decoration becoming reddish brown from handling, cylindric or narrowing upward or broadest at mid-stipe or narrowest at mid-stipe, flaring at apex or not; *bulb* (30–) 57–112+ × 17–40 mm [shortest in mature specimen of Mueller 4368], napiform to narrowly napiform or dauciform, radicating, varying from poorly differentiated from stipe to subabrupt; *context* white to sordid white [bruising light yellow only in Mueller 4368], solid (under some conditions center of stipe becoming water soaked or gelatinized and pale sordid yellowish tan), sometimes with lacunae in center (especially in large specimens), infrequently becoming hollow [e.g., in Mueller 4368], concolorous to pale pallid brown or pale pinkish brown or ochraceous or pale brick-colored in larval tunnels; *partial veil* apical to superior, white becoming gray above, occasionally with edge darker gray in age, below bearing gray pulverulence, striate above, skirt-like, submembranous to floccose-felted, tearing, often left as floccose patches over lamellae; *universal veil* absent or as pyramidal warts or patches placed irregularly or subconcentrically arranged in few to many (up to 10 or more) rows near broadest point of bulb or for as much as upper three-quarters of bulb length, often with underlying context forming white to pale grayish recurved scales with universal veil remnants on tips of such scales, rather dark brownish gray (5.6YR 3.4/0.9), with limbus internus sometimes as thick, loosely attached, friable ring at stipe base (then concolorous with stipe).

*Odor* lacking or similar to nutmeg at first; in age, “old ham”-type, but more penetrating and unpleasant. [“Musty” in Mueller 4368.] *Taste* not distinctive.

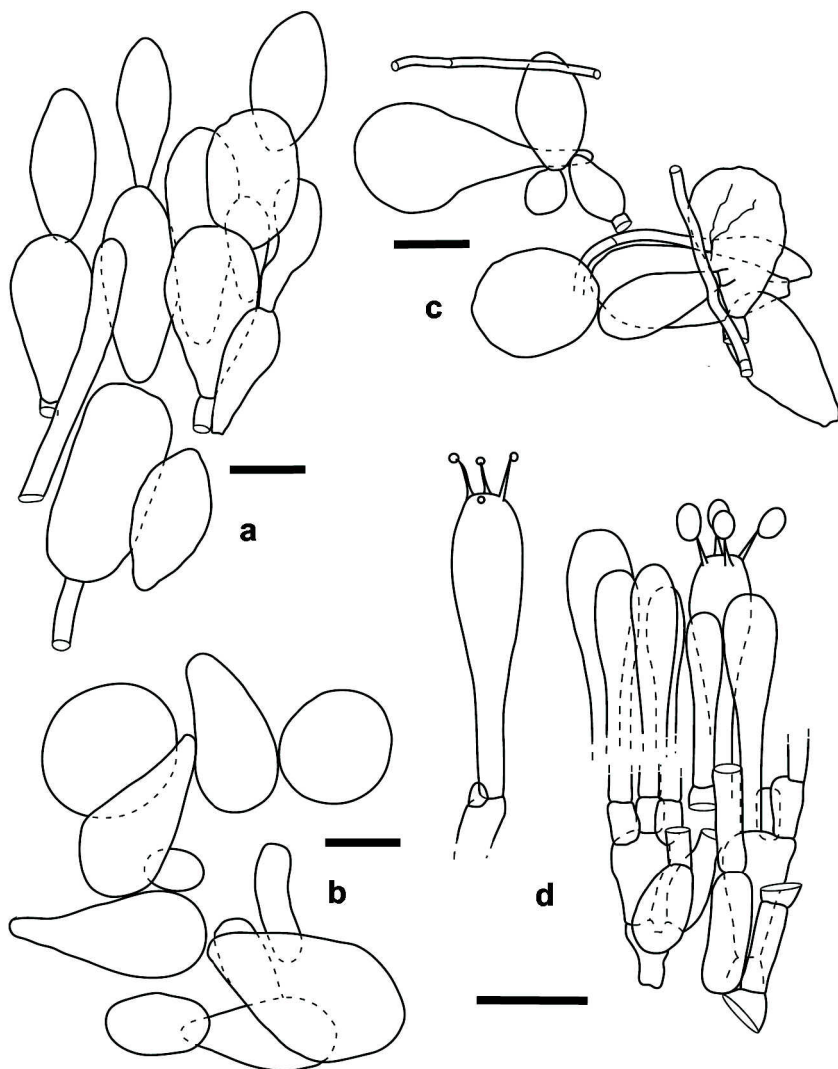


Fig. 11. *Amanita costaricensis*. a. Elements of universal veil from pileus wart (Tulloss 6-23-95-M). b. Elements of universal veil from floccose material of stipe (isotype). c. Elements of weakly structured partial veil (isotype). d. Elements of hymenium and subhymenial tree. Scale bars 20  $\mu$ m.

**MACROCHEMICAL TESTS:** Spot test for laccase (syringaldazine): negative throughout basidiome except for very few spots on margins of lamellae. Spot

test for tyrosinase (paracresol): negative throughout basidiome. Test voucher: Tulloss 6-20-95-A.

**PILEIPELLIS:** 315–460  $\mu\text{m}$  thick overall (175–235  $\mu\text{m}$  in old specimen); suprapellis 95–230  $\mu\text{m}$  thick (40–100  $\mu\text{m}$  in old specimen), partially gelatinized, pale yellow to colorless except (occasionally) dark brownish orange at surface; subpellis 160–260  $\mu\text{m}$  thick (130–135  $\mu\text{m}$  in old specimen), ungelatinized, dark brownish orange; filamentous undifferentiated hyphae 2.8–8.4  $\mu\text{m}$  wide, branching, densely packed, dominantly subradially oriented, but with some criss-crossing; vascular hyphae 7.4–21  $\mu\text{m}$  wide, scattered to locally common, sinuous, with those of largest diameter from old (senescent?) specimen (Gómez & Alfaro 20641). **PILEUS CONTEXT:** filamentous undifferentiated hyphae 2.0–20  $\mu\text{m}$  wide (many with width ca. 8.0  $\mu\text{m}$ ), branching, dominating, singly and in fascicles interwoven in open lattice, occasionally with yellowish subrefractive walls; inflated cells clavate to narrowly clavate to subfusiform, up to  $138 \times 34 \mu\text{m}$ , apparently mostly intercalary, one clavate cell terminal [possibly fitting definition of “acrophysalide” per Bas (1975)] except for hypha branching from one side, with walls thin or slightly thickened; vascular hyphae 8.4–31  $\mu\text{m}$  wide, occasionally branching, sinuous, scattered to locally common especially just below pileipellis, locally in loose knots, with those of largest diameter from old (senescent?) specimen (Gómez & Alfaro 20641). **LAMELLA TRAMA:** bilateral, divergent;  $w_{cs} = 45\text{--}60^{\pm} \mu\text{m}$  (moderate rehydration); central stratum composed largely of rather broad hyphae, apparently lacking intercalary inflated segments; subhymenial base comprising filamentous undifferentiated hyphae and narrow intercalary inflated cells (ellipsoid to obclavate to subfusiform to cylindric, up to  $90 \times 28 \mu\text{m}$ , singly and in short chains, with width predominantly 17.0–28  $\mu\text{m}$ ) diverging in smooth curve and achieving marked angle to central stratum; filamentous undifferentiated hyphae 2.8–10.2  $\mu\text{m}$  wide, branching, sometimes constricted at septa; divergent, terminal inflated cells not observed; vascular hyphae not observed. **SUBHYMENIUM:**  $w_{st\text{-}near} = 65\text{--}85 \mu\text{m}$  (poor to moderate rehydration) or 145–150  $\mu\text{m}$  (good rehydration);  $w_{st\text{-}far} = 85\text{--}110^{\pm} \mu\text{m}$  (poor to moderate rehydration) or 170–175  $\mu\text{m}$  (good rehydration); appearing pseudoparenchymatous in some regions, comprising 2–4 layers of inflated cells (sometimes dominating) and irregularly branched partially inflated to inflated elements and partially inflated (proportionately small) hyphal segments, with basidia arising from cells of all types. **BASIDIA:** (21–) 39–63  $\times$  (6.2–) 8.2–14.2 (–15.8)  $\mu\text{m}$ , thin-walled, 4-sterigmate, with sterigmata up to  $6.0 \times 2.8 \mu\text{m}$  or larger; clamps common. **UNIVERSAL VEIL:** *On pileus:* elements having strong vertical orientation except in base of wart; filamentous undifferentiated hyphae 1.0–13.6  $\mu\text{m}$  wide, branching, common in upper part

of wart, dominating in shallow interwoven layer at base of wart and there periclinally oriented and more often in fascicles, sometimes constricted at septa, colorless at first becoming orange-brown like inflated cells; inflated cells pale brown to pale brownish gray to pale gray, becoming brownish orange to orange-brown to brown,  $28\text{--}128 \times 11.5\text{--}50\text{ }\mu\text{m}$ , dominating except in base of wart, terminal in short chains, thin-walled, subglobose to broadly ellipsoid to ellipsoid to broadly clavate (up to  $83 \times 50\text{ }\mu\text{m}$ ) or basidiiform to narrowly clavate to subcylindric to cylindric to subfusiform (up to  $128 \times 37\text{ }\mu\text{m}$ ), all forms occasionally rostrate when in terminal position in chain; vascular hyphae  $7.2\text{--}10.2\text{ }\mu\text{m}$  wide sinuous, infrequent, scattered. *On mid-stipe region*: almost entirely comprising scattered inflated cells, ungelatinized to partially gelatinized to gelatinized, subglobose (e.g.,  $32 \times 28\text{ }\mu\text{m}$ ), ellipsoid (e.g.,  $38 \times 26\text{ }\mu\text{m}$ ), narrowly to broadly clavate (e.g.,  $56 \times 33\text{ }\mu\text{m}$ ), bacilliform (e.g.,  $32 \times 8.6\text{ }\mu\text{m}$ ). *On bulb of stipe*: comprising disordered elements, with greater proportion of filamentous undifferentiated hyphae than in universal veil on pileus, otherwise similar to remnants on pileus. *STIPE CONTEXT*: longitudinally acrophysalidic; filamentous undifferentiated hyphae  $1.9\text{--}9.9\text{ }\mu\text{m}$  wide, plentiful, occasionally branching; acrophysalides plentiful, up to  $406 \times 33\text{ }\mu\text{m}$ ; vascular hyphae  $7.0\text{--}16.5\text{ }\mu\text{m}$  wide, infrequent, sinuous, yellowish, mostly near exterior surface. *PARTIAL VEIL*: with hyphae, elongate cells, and rows of cells sometimes subradially oriented; radially streaked on upper surface with partially gelatinized collapsed remains of lamella edge tissue; filamentous undifferentiated hyphae  $1.5\text{--}7.5\text{ }\mu\text{m}$  wide, moderately common, branching occasionally, often single, sometimes in narrow fascicles, infrequently in fascicles up to  $17.5\text{ }\mu\text{m}$  wide; inflated cells arising from nonvascular hyphae (see below for inflated cells arising from vascular hyphae) thin-walled, terminal, singly or in short chains (mostly of two), pyriform or ovoid or elongate or ellipsoid or subfusiform or subcylindric or broadly clavate or clavate or narrowly clavate, up to  $113 \times 29\text{ }\mu\text{m}$ , occasionally with yellowish walls, dominantly colorless, hyaline; vascular hyphae  $2.8\text{--}5.0\text{ }\mu\text{m}$  wide, very infrequent, infrequently giving rise to yellow-walled terminal cell (elongate to ellipsoid, up to  $26 \times 22\text{ }\mu\text{m}$ ). *LAMELLA EDGE TISSUE*: sterile.

*BASIDIOSPORES*:  $[321/16/10]$   $(7.5\text{--})\ 8.5\text{--}13.2\text{ (}\text{--}16.0\text{)} \times (5.1\text{--})\ 6.0\text{--}8.5\text{ (}\text{--}12.6\text{)}\text{ }\mu\text{m}$ , ( $L = (9.1\text{--})\ 9.4\text{--}12.3\text{ }\mu\text{m}$ ;  $L' = 10.8\text{ }\mu\text{m}$ ;  $W = 6.4\text{--}7.7\text{ (}\text{--}8.3\text{)}\text{ }\mu\text{m}$ ;  $W' = 7.2\text{ }\mu\text{m}$ ;  $Q = (1.10\text{--})\ 1.27\text{--}1.83\text{ (}\text{--}2.15\text{)}$ ;  $Q = 1.35\text{--}1.68\text{ (}\text{--}1.70\text{)}$ ;  $Q' = 1.51$ ), hyaline, colorless, smooth, thin-walled, amyloid, acyanophilous, dominantly ellipsoid to elongate, infrequently broadly ellipsoid or cylindric, often at least somewhat adaxially flattened, occasionally expanded at one end; apiculus sublateral, small, cylindric; contents mono- to multiguttulate to granular; white in deposit.

**ECOLOGY:** Solitary to subgregarious. Costa Rica: At 1715–2500 m elev. In *Quercus-Magnolia* forest or in mixed *Quercus* forest sometimes with *Q. oocarpa* dominant. Honduras: At 1900± m elev. In cloud forest with *Quercus trichodonta* and other hardwoods.

**MATERIAL EXAMINED:** **COSTA RICA:** CARTAGO—San Cristobal, vii.1983 L.D. Gómez & R. Alfaro 21222 (F 1100824). GUANACASTE—Cacao no. 1, sendero a derrumbe, 3.vi.1996 C. Cano 197 (INBio; RET 325-4). SAN JOSÉ—La Chonta, v.1982 L.D. Gómez 18147 (F 1051869); Jaboncillo de Dota, 20.vi.1995 R.E. Halling & K. Shanks s.n. [Tulloss 6-20-95-A] (RET 330-3; USJ); El Jardín de Dota, vii.1983 L.D. Gómez & R. Alfaro 20641 (F 1073283); San Gerardo de Dota no. 1, 26.vii.1992 B. A. Strack, L.D. Gómez, G. Hewson & G.M. Mueller [Mueller 4398] (F 1102451), 21.vi.1995 R.E. Halling s.n. [Tulloss 6-21-95-M] (holotype, USJ; isotype, RET 330-4), 23.vi.1995 Thomas O'Dell s.n. [Tulloss 6-23-95-M] (RET 330-5; USJ); San Gerardo de Dota no. 4, 24.vii.1992 B.A. Strack, J. Polishook, L.D. Gómez, G. Hewson & G.M. Mueller [Mueller 4368] (F 1102421). **HONDURAS:** FRANCISCO MORAZAN—Mt. Uyuca, Valle Zamorano, 5.vii.1991 G.M. Mueller, B.A. Strack, R. & M. Singer & R. Andino [Mueller 4138] (F 1098682). OLANCHO—ca. Campamento, P.N. La Tigre, rd. to Finca Sapote, 9.vii.1991 G.M. Mueller, B.A. Strack, R. & M. Singer & R. Andino [Mueller 4182] (F 1098725).

**COMMENTS** — This species was described in the notebooks of the late Dr. Rolf Singer under his herbarium name “*costaricensis*.” Since he originated the name and had a clear concept of its application and since we utilize collections annotated by him, we have included Dr. Singer as an author of the species.

According to the descriptions and keys of Bas (1969), *A. costaricensis* fits well within his stirps *Microlepis* of *Amanita* [sect. *Lepidella*] subsect. *Solitariae* Bas. Within this stirps, the present species is strikingly similar to *A. atkinsoniana* Coker (Coker 1917) and *A. onusta* (Howe) Sacc. (Saccardo 1891).

*Amanita atkinsoniana* (Tulloss 2011d) is moderately common in a range extending from southern Prov. Québec, Canada (Pomerleau 1980) to Michoacan edo., Mexico. *Amanita atkinsoniana* can be distinguished from the present species by

- smaller spores—[230/10/10] (6.8–) 8.0–10.5 (–14.3) × (5.0–) 5.4–7.2 (–8.5) µm, (**L** = (8.2–) 9.0–9.7 µm; **L'** = 9.2 µm; **W** = 5.7–6.6 (–6.9) µm; **W'** = 6.2 µm; **Q** = (1.17–) 1.27–1.71 (–1.95); **Q** = 1.36–1.57 (–1.67); **Q'** = 1.50)
- basidiome generally white or pallid except for universal veil, with universal veil in fine distinctly separated warts (grayish at first, then reddish brown) on pileus, with basal bulb usually napiform or turbinate, with universal veil brownish gray becoming reddish brown and distributed in rather fine warts in at least six (6) concentric rings around the stipe's bulb from its top to (often) well below mid-length of the bulb,

with fragile apical to subapical partial veil, which (when it persists) may become slimy and yellow while remaining in a superior position on the stipe

- scattered, minimal, positive spot tests for tyrosinase—with L-tyrosine, slowly positive on surfaces of lower stipe and upper bulb (possibly in association with universal veil material in those areas) and in pileipellis.

**MATERIAL EXAMINED** (*Amanita atkinsoniana*): **MÉXICO**: MICHOACAN—Parq. Nac. "Insurgente José Ma. Morelos," Mpio. Charo, 19.viii.1983 Reza Araujo s.n. (FCME). **U. S. A.**: CONNECTICUT—Middlesex Co. – E. Haddam, Devil's Hop Yard St. Pk., 25.ix.1999 Arnold s.n. [Tulloss 9-25-99-P] (RET 301-1); Meshomasic St. For., 19.ix.1998 Peter Kukle s.n. [Tulloss 9-19-98-A] (RET 288-2). **MAINE**—Cumberland Co. – S. Windham, 25.viii.1984 S.S. Ristich s.n. [Tulloss 8-25-84-SSR-A] (RET 235-6). **MASSACHUSETTS**—Berkshire Co. – Pittsfield St. For., 16.viii.1986 Wes Faust s.n. [Tulloss 8-16-86-G] (RET 137-7). **NEW JERSEY**—Morris Co. – Hacketstown Reservoir, 13.viii.1984 Robert Peabody & Roger Phillips s.n. [Tulloss 8-13-84-PPA] (RET 113-8). **NEW YORK**—Dutchess Co. – Thompson Pond Preserve, Pine Plains, 4.viii.1996 Wm. Bakaitis s.n. (NYS D1592). **NORTH CAROLINA**—Granville Co. – Butner, John Umstead Hospital picnic area, 18.xi.1994 Owen L. McConnell s.n. (RET 139-6). McDowell Co. – ca. Little Switzerland, Wildacres Resort, 27.ix.2008 J. Justice NC-AM12 (RET 445-1). Orange Co. – Chapel Hill, Battle's Pk., 14.ix.1913 W.C. Coker 759 (holotype, NCU, mixed collection segregated by C. Bas). **WEST VIRGINIA**—Greenbrier Co. – Monongahela Nat. For., Lake Sherwood, 31.viii.1982 R.E. Tulloss 8-31-82-D (RET 226-2). Tucker Co. – Dolly Sods, 1.viii.1985 W. Sturgeon s.n. [Tulloss 8-1-85-BJ] (RET 201-6).

*Amanita onusta* (Tulloss 2011e) is a locally common species of eastern North America with a range extending from Prov. Québec (Pomerleau 1980) and Prov. Nova Scotia (Stewart & Grund 1974), Canada at least to Illinois and Mississippi, USA. (Tulloss unpub. data). *Amanita onusta* can be distinguished from the present species by

- smaller spores—[215/12/12] (7.0–) 8.0–11.0 (–13.0) × (5.0–) 5.5–7.0 (–8.3)  $\mu\text{m}$ , ( $L = 8.3\text{--}10.5$  (–11.0)  $\mu\text{m}$ ;  $L' = 9.4$   $\mu\text{m}$ ;  $W = 5.7\text{--}6.5$  (–7.1)  $\mu\text{m}$ ;  $W' = 6.1$   $\mu\text{m}$ ;  $Q = (1.14\text{--}) 1.28\text{--}1.85$  (–2.21);  $Q = 1.35\text{--}1.65$  (–1.84);  $Q' = 1.52$ )
- basidiomes paler and with little (if any) brown tint, frequently of smaller size with pileus often less than 40 mm wide [13–76 mm wide in Tulloss' experience, although Bas (1969) reports at least one instance of a specimen with pileus over 100 mm wide], with lamellae that rather rapidly become yellowish and show signs of decay while the remainder of the basidiome shows none, and often without a persistent partial veil
- positive spot tests for tyrosinase—with L-tyrosine, positive, throughout the basidiome and, with paracresol, positive in scattered spots in very

young material, positive in pileus context and context of stipe above bulb in older material.

MATERIAL EXAMINED (*Amanita onusta*): U. S. A.: CONNECTICUT—Litchfield Co. – Black Rock St. Pk., 10.viii.1983 D.C. & R.E. Tulloss 8-10-83-A (RET 104-8). MAINE—Sagadahoc Co. – Woolwich, 7.x.1995 S.S. Ristich s.n. (RET 159-7). NEW JERSEY—Mercer Co. – Hightstown, 22.vii.1981 R.E. Tulloss 7-22-81-B (RET 106-9). Monmouth Co. – Upper Freehold Twp., Assumpink Wildlife Mgt. Area, Roosevelt Rd., 21.vii.1981 R.E. Tulloss 7-21-81-E (RET 163-3), 4.viii.1981 R.E. Tulloss 8-4-81-A (RET 109-6), 18.ix.1981 M.A. King & R.E. Tulloss 9-18-81-E (RET 164-7), 11.vii.1982 D.C., M.H., & R.E. Tulloss 7-11-82-B (RET 340-10). Morris Co. – Morristown, 27.viii.1981 Al Northrup s.n. [Tulloss 8-27-81-AN] (RET 166-10). VIRGINIA—Franklin Co. – ca. Ferrum, ca. Ferrum College, 4.viii.1982 Gerald Bills, Pierre Dery, O.K. & H.H. Miller OKM19946 (VPI, as "*A. peckiana*"). WEST VIRGINIA—Marion Co. – Mill Fall Run, 21.ix.1992 R.P. Bhatt A2 (FWVA).

In two cases [Halling 7667 (NY; USJ) and Tulloss 6-21-95-E (RET 337-3; USJ)], an amanita assignable to *Amanita* subgenus *Lepidella* (sect. *Validae* or sect. *Lepidella*) was misdetermined in the field as *A. costaricensis*. The undetermined species has a gray stipe that is stuffed (becoming hollow), gray underside and margin to the membranous annulus, gray warts on the gray-brown to pale gray pileus, and short basidia [19–34 (–44)  $\mu\text{m}$  long] apparently lacking clamps. The species is somewhat unusual for sect. *Validae* because of its unpleasant smell (sometimes like the smell of disinfectant cleaning solution in hospitals). The misdetermined entity should be distinguishable by the lack of a radicating bulb, the absence of basidial clamps, and by its smaller and more nearly globose spores: [33/2/2] (7.3–) 7.5–9.0 (–10.0)  $\times$  (6.5–) 7.0–8.0 (–9.1)  $\mu\text{m}$ , (**L** = 8.2  $\mu\text{m}$ ; **L'** = 8.2  $\mu\text{m}$ ; **W** = 7.5  $\mu\text{m}$ ; **W'** = 7.5  $\mu\text{m}$ ; **Q** = (1.04–) 1.05–1.14 (–1.23); **Q** = 1.09–1.11; **Q'** = 1.09). Especially, considering the apparently parasitized collections of *A. costaricensis* discussed below, we had some hesitation concerning whether or not Halling 7667 and Tulloss 6-21-95-E also comprised parasitized material. However, we are convinced that they represent a distinct species because (1) the spores of these two collections were both shorter (on average) and broader (on average) than those of *A. costaricensis* [Compare values of **L'** and **W'**. Reduction in spore volume due to stress would have reduced both length and width.]; (2) both exhibited a membranous annulus; and (3) both apparently lack basidial clamps. Basidia predominantly less than 30  $\mu\text{m}$  long, might support assignment to sect. *Validae*, but further study is required.

In one case {Estrella, 14.vi.1996 R.E. Halling & J. Ammirati [Halling 7684] (NY; USJ)}, all the specimens of a rather large collection apparently assignable to *A. costaricensis* had an odor like pig manure. In addition, some had rather distorted stipes; and the spores of all collections were uniformly smaller

than normal ([100/5/1] (7.2–) 7.6–9.5 (–11.0)  $\times$  (5.3–) 5.5–7.3 (–8.0)  $\mu\text{m}$ , (**L** = 8.3–9.0  $\mu\text{m}$ ; **L'** = 8.7  $\mu\text{m}$ ; **W** = 6.2–6.6  $\mu\text{m}$ ; **W'** = 6.4  $\mu\text{m}$ ; **Q** = (1.18–) 1.23–1.50 (–1.80); **Q** = 1.30–1.45; **Q'** = 1.37). Observed at 1250 $\times$ , many of the spores were surrounded with small, hyaline, colorless, inamyloid spheres (1 $\pm$ –3 $\pm$   $\mu\text{m}$  diam.) connected to the spore walls by what appeared to be fine tubules—the whole having the appearance of a pincushion. We hypothesize that the noted alterations in morphology and odor are a result of “parasitization.” The authors explicitly exclude Halling 7684 from the set of paratypes.

In another case of apparent parasitization (San Gerardo de Dota no. 4, 24.vii.1992 B.A. Strack, J. Polishook, L.D. Gómez, G. Hewson & G.M. Mueller [Mueller 4368] (F 1102421)), spores, basidia, and lamella trama were quite normal for the species; however, the context of both the pileus and stipe stained yellow when cut. Two other pigment-related characters were unusual for *A. costaricensis* as we understand it: universal veil remnants on pileus, stipe, and bulb of stipe were paler than usual and remained paler than the pileus disc despite becoming brown with time, even in a mature specimen; and the pileus disc was darker than usual. Further, lamellulae were reported to all be very short; and the basidiomes were said to have had an unusual musty odor. The yellow staining is very similar to that seen in apparently parasitized specimens of *A. subsolitaria* (Murrill) Murrill from the Atlantic coastal plain of the USA (Tulloss 1998b; 2000a: 57, fig. 5; Tulloss 2011c). In the latter case, basidiomes are sometimes found that not only stain bright yellow when cut, but release an orange-amber liquid from wounds. Spores of such specimens are often, but not always, subnormal in size and distorted in shape—the same yellowing phenomenon may be seen in specimens with spores nearly, or quite, normal with regard to size and shape. The provisional name of Bas (1969), *A. “crassifolia,”* was put forward for yellowing material that Bas thought might be determinable as *A. subsolitaria*; Tulloss is now convinced this is the case.

It should be noted that two North American taxa assignable to sect. *Lepidella* have been described by Bas (1969) because of their pronounced ability to become bright yellow or yellow-orange when cut (*A. cinereoconia* var. *croceescens* Bas and *A. rhoadsii* var. *flavotिंगens* Bas). Tulloss (1998b, 2000a) questioned whether these entities might not be based on parasitized specimens of the respective species. It would be interesting to see what information about *Amanita* parasites might be determined from study of fresh material of Costa Rican cases of apparent parasitization such as those presented above. If the species with yellowing context reaction in sect. *Lepidella* may be grouped together and the yellowing attributed to a single cause, or a set of common causes, then *A. costaricensis* becomes the first representative of this group in

Bas' stirps *Microlepis*. We have included Mueller 4368 as a paratype because microscopic examination produced observations completely consistent with "normal" material of *A. costaricensis*. In the macroscopic description of *A. costaricensis*, the unusual characters of Mueller 4368 are so labeled.

Mueller 4398 consists of a single immature specimen with the partial veil covering the lamellae.

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# Appendix: Gazetteer of collecting sites in Costa Rica referenced in this and planned future studies on *Amanita*

Localities are designated by uncomplicated names in the taxonomic part of this paper. Full site descriptions with latitude, longitude, elevation, and the species of *Quercus* present at the site (where data is available) are provided in the following table. Full data was sometimes not available because of the difficulty of interpreting herbarium labels on collections made prior to the current projects. Most of our data comes from the latter. Also, milestones along the Interamerican Hwy. have been moved over time, and the mention of a milestone in an old locality description may be less accurate than the apparently less precise or more informal part of the description. The issue of incompletely documented sites arises largely because of the number of good quality "historic" collections in F. Latitude, longitude, and elevation for recently explored sites were determined by use of a Garmin (GPS75) device.

| Site Name             | Site Description<br>(including Oaks Present)                                                      | Lat./Long.,<br>Elevation                  |
|-----------------------|---------------------------------------------------------------------------------------------------|-------------------------------------------|
| <b>PROV. ALAJUELA</b> |                                                                                                   |                                           |
| 1. Bosque del Niño    | Ctn. Grecia, Grecia, Bosque del Niño<br>- <i>Q. seemannii</i> (dominant)                          | 10°9'4"N/84°14'42"W,<br>1900 m elev.      |
| 2. Palmira            | ?<br>- no data on oaks                                                                            | ca. 10°12'N/84°23'W,<br>no data on elev.  |
| <b>PROV. CARTAGO</b>  |                                                                                                   |                                           |
| 3. Cañon              | ca. Cañon, E of Interam. Hwy., at<br>La Esperanza del Guarco<br>- <i>Q. copeyensis</i> (dominant) | 9°41'1"N/83°52'43"W,<br>2505 m elev.      |
| 4. Estrella           | 5 km E of km 31 of Interam. Hwy.,<br>ca. Estrella<br>- <i>Q. oocarpa</i> , <i>Q. seemannii</i>    | 9°46'4"N/83°57'19"W,<br>1685-1717 m elev. |
| 5. Palo Verde         | 4± km E of km 31 of Interam. Hwy.,<br>ca. Palo Verde<br>- <i>Q. oocarpa</i>                       | 9°46'34"N/83°56'42"W,<br>1600 m elev.     |
| 6. [unnamed]          | off Interamerican Hwy., 6 km S of Cartago at rd. to Palo Verde<br>- no data on oaks               | ?,<br>? m elev.                           |
| 7. Prusia             | Parque Prusia, W slope of Volcán Irazu<br>- <i>Q. costaricensis</i>                               | 9°57'56"N/83°52'15"W,<br>2900 m elev.     |
| 8. San Cristobal      | unknown site along Interam. Hwy.<br>- no data on oaks                                             | ?,<br>2000 m elev.                        |
| 9. Sanatorio          | ?<br>- no data on oaks                                                                            | ?,<br>? m elev.                           |

| Site Name                                      | Site Description<br>(including Oaks Present)                                                                                                                     | Lat./Long.,<br>Elevation                  |
|------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------|
| 10. Tapanti                                    | Guarco, Tapanti, P. N. Tapanti,<br>Macizo de la Muerte,<br>Área de Conservación La Amistad<br>Pacífico<br>- <i>Q. copeyensis</i>                                 | 9°4'6"N/83°52'30"W,<br>2600 m elev.       |
| PROV. GUANACASTE<br>11. Cacao no. 1            | Cerro Pedregal,<br>Estación Biología Cacao,<br>Área de Conservación Guanacaste<br>- <i>Q. brenesii</i>                                                           | 10°55'45"N/85°28'37"W,<br>1100 m elev.    |
| 12. Cacao no. 2                                | Cerro Cacao, Estación Biología Cacao,<br>Área de Conservación Guanacaste<br>- <i>Q. brenesii</i>                                                                 | 10°56'8"N/85°27'14"W,<br>1000 m elev.     |
| PROV. HEREDIA<br>13. San José de la<br>Montaña | Volcán Barva, Paso Llano, San José de la<br>Montaña<br>- no data on oaks                                                                                         | ca. 10°3'N/84°7"W,<br>2100 m elev.        |
| PROV. PUNTARENAS<br>14. Finca Las Alturas      | Ctn. Coto Brus, Finca Las Alturas,<br>Standford Biol. Field Stn.,<br>tr. to Cerro Echandi<br>- no data on oaks                                                   | ?,<br>1700 m elev.                        |
| 15. La Amistad no. 1                           | Ctn. Coto Brus, La Amistad, Zona<br>Protectora Las Tablas, Finca La<br>Cafrosa, Camino El Portones por El<br>Tajo<br>- <i>Q. corrugata</i> & <i>Q. seemannii</i> | 8°55'34"N/82°46'0"W,<br>1350–1500 m elev. |
| 16. La Amistad no. 2                           | Ctn. Coto Brus, Las Mellizas,<br>La Amistad Lodge,<br>ca. P. N. La Amistad<br>- <i>Q. corrugata</i> & <i>Q. seemannii</i>                                        | 8°54'52"N/82°46'50"W,<br>1380 m elev.     |
| 17. San Vito                                   | Ctn. Coto Brus, San Vito de Coto Brus,<br>5 km W of Jardín Botánico Las Cruces<br>- no data on oaks                                                              | ca. 8°49'N/83°0'W,<br>1500 m elev.        |
| PROV. SAN JOSÉ<br>18. Alto de la Palma         | Ctn. Guadalupe, Alto de la Palma, ?<br>- no data on oaks                                                                                                         | ?,<br>? m elev.                           |
| 19. C.A.T.I.E. For.                            | Ctn. Perez Zeledón, Villa Mills,<br>C.A.T.I.E. Exp. For. of Villa Mills<br>- <i>Q. costaricensis</i>                                                             | 9°33'3"N/83°40'55"W,<br>2880 m elev.      |

| Site Name                        | Site Description<br>(including Oaks Present)                                                                                                                                                                           | Lat./Long.,<br>Elevation                         |
|----------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|--------------------------------------------------|
| 20. Copey de Dota                | Ctn. Dota, Copey de Dota 12 km S of<br>Copey on rd. to Providencia<br>- <i>Q. copeyensis</i>                                                                                                                           | 9°35'19"N/83°53'3"W,<br>2800 m elev.             |
| 21. El Empalme                   | Ctn. Dota, 200± m W of Interam. Hwy. at<br>El Empalme, La Guaria [Note: Site<br>has been completely logged.]<br>- <i>Q. copeyensis</i>                                                                                 | 9°43'8"N/83°57'4"W,<br>2250 m elev.              |
| 22. Finca Alejandrina            | Ctn. Perez Zeledón, Villa Mills, Finca<br>Alejandrina, Interam. Hwy. km 95, ca.<br>Hotel La Georgina<br>- <i>Q. costaricensis</i>                                                                                      | 9°33'43"N/83°44'22"W,<br>3000 m elev.            |
| 23. Jaboncillo de Dota           | Ctn. Dota, Jaboncillo de Dota, 3.2 km<br>from Interam. Hwy on rd. to San<br>Gerardo de Dota<br>- <i>Q. copeyensis</i>                                                                                                  | 9°35'21"N/83°47'58"W,<br>2740 m elev.            |
| 24. Jardín de Dota               | Ctn. Dota, 3.5 km W of Interam.<br>Hwy. at El Empalme<br>- <i>Q. copeyensis</i> , <i>Q. seemannii</i> (occas.)                                                                                                         | 9°42'52"N/83°58'28"W,<br>2220 m elev.            |
| 25. La Chonta                    | Ctn. Dota, S of Interam.<br>Hwy. twd. Cerro Chonta<br>- <i>Q. copeyensis</i> , <i>Q. seemannii</i> , <i>Q.<br/>rapurahuensis</i>                                                                                       | 9°41'58"N/83°56'31"W,<br>2400 m elev.            |
| 26. San Gerardo de<br>Dota no. 1 | Ctn. Dota, San Gerardo de Dota,<br>5± km SW of Cerro de la Muerte,<br>Albergue de Montaña Savegre (Cabi-<br>nas Chacón)<br>- <i>Q. copeyensis</i> , <i>Q. seemannii</i> , <i>Q.<br/>rapurahuensis</i>                  | 9°33'2"N/83°48'27"W,<br>2200 to ca. 2350 m elev. |
| 27. San Gerardo de<br>Dota no. 2 | Ctn. Dota, 500 m from Interam. Hwy. on<br>rd. to San Gerardo de Dota<br>- <i>Q. costaricensis</i>                                                                                                                      | 9°36'13"N/83°47'26"W,<br>3000 m elev.            |
| 28. San Gerardo<br>de Dota no. 3 | Ctn. Dota, 1.5 km from Interam. Hwy.<br>on rd. to San. Gerardo de Dota<br>- <i>Q. copeyensis</i> , <i>Q. costaricensis</i>                                                                                             | 9°35'47"N/83°47'55"W,<br>2860 m elev.            |
| 29. San Gerardo<br>de Dota no. 4 | Ctn. Dota, off Interam. Hwy., 2–3 km S<br>of Cerro de la Muerte, rd. to San<br>Gerardo de Dota<br>- no field data on oaks; <i>Q. copeyensis</i> and<br><i>Q. rapurahuensis</i> likely, <i>Q. seemannii</i><br>possible | ?,<br>btwn. 2200 to 2860 m<br>elev.              |